Responses of Great Bustard (*Otis tarda*) subpopulations to land-use changes in southwestern Iberia

Yoav Perlman

Thesis submitted for the degree of Doctor of Philosophy

School of Environmental Sciences

University of East Anglia

April 2018

Table of Contents

Abstract

Land-use change is the single most important cause of global biodiversity loss. Over millennia, European grassland birds concentrated in low-intensity agro-steppe habitats that are now experiencing intensification largely in line with European market forces. Great Bustard (*Otis tarda,* GB) is a globally threatened species and a symbol of the Iberian agro-steppes. In Extremadura (Spain) and Alentejo (Portugal) the conservation status of GB and other agro-steppe species is unclear. GB subpopulations were monitored in these two regions between 1985 and 2015, and their trends were related to land-use changes using open-access databases. There was regional variation in trends, and I report here a sharp decline in numbers across the study area since 2010. Trends were not related to moderate reduction of agro-steppe habitats, but were negatively related to changes in livestock densities, implying that livestock management of habitats is crucial for conservation. Using field counts in spring 2017 across a network of EU Special Protected Areas (SPAs) designated to protect GB, I found that GB is not a good indicator for other agro-steppe species of conservation concern. Selection of further indicator species is recommended for better conservation of agro-steppe bird assemblage. In an SPA in Extremadura, GB productivity rates decreased dramatically between 2005 and 2016. If current productivity rates continue, population modelling predicts a steep decline in numbers at this site. Results of this study raise concerns over the function of the SPA network in Extremadura and Alentejo to protect GB and their agro-steppe habitat. To sustain numbers of GB and other agro-steppe species, their habitats need to be better protected from further intensification, including control of livestock densities, preferably using agro-environmental schemes in PAs.

Acknowledgments

First, I want to thank my supervisors, primarily Paul Dolman. Throughout my PhD journey, my supervisors pushed me forward, demanded the highest academic and scientific standards possible, and for that I am grateful. Their relentless quest to achieve excellence in science was inspirational and educational. I am especially grateful to João Paulo Silva and to Nigel Collar, who introduced me to their study systems in Extremadura and Alentejo, built bridges and formed connections with key people that were essential for my research. João Paulo Silva also opened his house to me; João and his lovely family really made me feel at home in Alentejo. Nigel Collar provided me with huge support during the final steps of my writing – thank you.

My main collaborators in Extremadura and Alentejo, Angel Sánchez from Junta de Extremadura, and Pedro Rocha from Instituto da Conservação da Natureza e das Florestas (ICNF), provided me not only with data, but also with warm hospitality and networking. Their support of my data and fieldwork efforts was essential for this study.

In Extremadura, Joaquín Dávalos from Junta de Extremadura assisted hugely with data interpretation. Agustín Mogena and Javier Caldera from ZEPA Llanos de Cáceres y Sierra de Fuentes provided much needed assistance; especially Agustín was extremely helpful with any queries I had, and for that I am grateful. Joachim Hellmich supplied data and joined me to his fieldwork team which was extremely important. Fergus Crystal and Marc Gálvez are dear friends who opened their houses to me and provided me with much help, for which I am extremely thankful.

In Alentejo, Marcia Pinto provided me with important insights regarding my research directions. In Alentejo, Liga para a Protecção da Natureza (LPN) staff at Centro de Educação Ambiental do Vale Gonçalinho (CEAVG) were extremely helpful, especially Rita Alcazar and Bruno Herlander Martins for their friendship and support, mainly during fieldwork.

Re'a Shaish and Dan Branch were excellent fieldwork assistants – they worked professionally, and we had a great time together. Martin and Claudia Kelsey generously offered us accommodation at their lovely Casa El Recuerdo; Martin also assisted hugely with fieldwork and with gathering information.

I thank Swarovski Optik for their ongoing support, in providing me with the best optics for fieldwork.

Back at UEA I am indebted to my fellow researchers at Centre for Ecology, Evolution and Conservation (CEEC). John Burnside and James Gilroy were always helpful and supportive, providing me with advice on issues simple and complex. John joined my supervisory team during my first year, and did an excellent job. My peers provided me with never-ending support through the years. Eleanor Warren-Thomas, Maxim Koshkin, Karen Hornigold, Phil Saunders, Anderson Saldanha Bueno, Valentina Zini, Agatha Nthenge, Marta Acácio, Kate Rogerson, Rob Hawkes, Nick Gerard and Claire Buchan – you guys are stars. You all provided me with important professional help, but most importantly with friendship and moral support, to which I am ever grateful.

Ian Lake and Sue Jickells supported me in unique ways during my PhD. Thank you.

Finally, my wife Adva, my kids Uri, Noam and Libby, and my extended family were my backbone through my PhD. Your love and support held me through tough times. Without you, my loved ones, I would not have completed this PhD.

Chapter 1

General Introduction

1.1 Land-use changes and the biodiversity crisis

With increasing global human population numbers and the pressure they place on ecosystems (Venter *et al.* 2016), land-uses are changing rapidly, to accommodate the population increase in numbers and consumption (Elmhagen *et al.* 2015; Steffen *et al.* 2004). With the continuing increase in human populations, global biodiversity is being lost rapidly, with extinction rates often referred to as 'The Sixth Extinction' (Fig. 1.1; Ceballos *et al.* 2015; Ceballos, Ehrlich, & Dirzo 2017; McCallum 2015). A global assessment estimated species richness declines of 13.6%, rarefaction-based richness declines of 8.1%, and total abundance declines of 10.7% 'compared to what they would have been in the absence of human effects' (Newbold *et al.* 2015). Although birds have not necessarily been more affected by land-use changes than other taxa (Pimm *et al.* 2006), they are well studied and can be used as indicators for broader biodiversity (Gregory *et al.* 2003; Lawton *et al.* 1998).

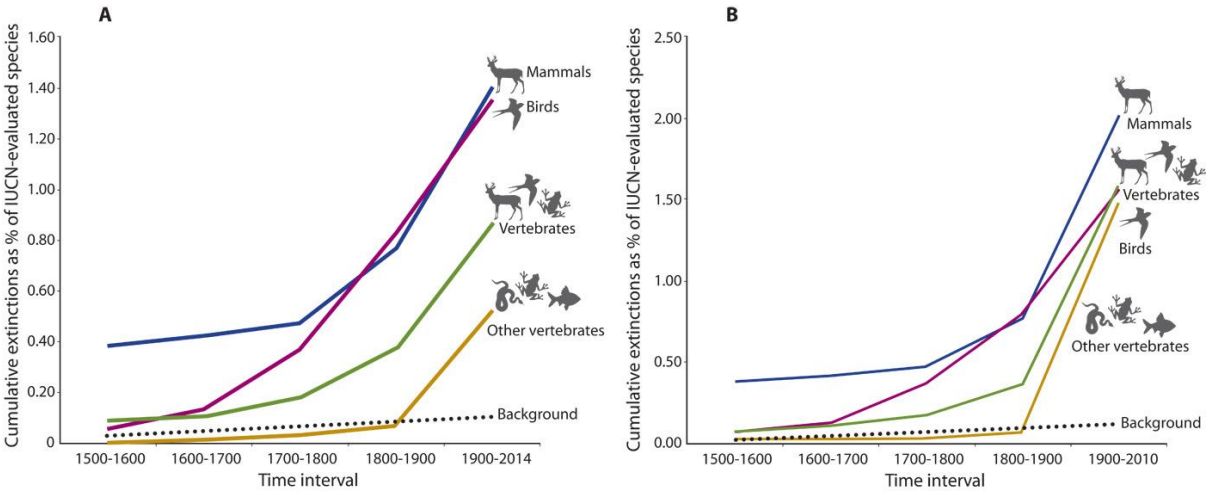


Figure 1.1: Cumulative vertebrate species recorded as extinct or extinct in the wild by the IUCN (2012). Graphs show the percentage of the number of species evaluated among mammals (5513; 100% of those described), birds (10,425; 100%), reptiles (4414; 44%), amphibians (6414; 88%), fishes (12,457; 38%), and all vertebrates combined (39,223; 59%). Dashed black curve represents the number of extinctions expected under a constant standard background rate of 2 E/MSY. (A) Highly conservative estimate. (B) Conservative estimate. Source: Ceballos *et al.* (2015) *Science Advances,* 1, DOI: 10.1126/sciadv.1400253

Land-use changes generally include conversion of natural habitats to anthropogenic land-uses, fragmentation, intensification of existing anthropogenic / semi-natural habitats, and degradation of natural habitats to systems that support lesser levels of biodiversity (Fahrig 2003; Foley *et al.* 2005; Hanski 2011; Mora & Sale 2011). Land-use change is the single biggest cause of current and projected biodiversity loss, with other significant factors being climate change, nutrient increase, exploitation and invasive species (Bellard *et al.* 2014; Doherty *et al.* 2016; Isbell *et al.* 2017; Mollot, Pantel, & Romanuk 2017) and their interactions (Mantyka-Pringle, Martin, & Rhodes 2012).

In Europe, agricultural land-use changes have shaped the structure of ecosystems for millennia. There is evidence of European landscape transformation

by humans thousands of years ago (Blondel, 2006; Klein Goldewijk*et al.* 2011). As a result, European biodiversity is mostly retained in low-intensity agricultural systems (Bignal & McCracken, 2000). During the 19th and 20th centuries, a marked change in European agricultural landscapes has been noted. Mutual processes of intensification and abandonment of agricultural systems, especially crop and livestock systems, resulting from local and global economic processes and social dynamics, alter the structure of agricultural landscapes (Queiroz *et al.* 2014; Reidsma *et al.* 2006; Thébault *et al.* 2014; van Vliet *et al.* 2015, Young *et al*, 2007). Protecting biodiversity in low-intensity agricultural systems has become a priority for European conservation authorities, often using agri-environmental schemes in High Nature farmland (Batáry *et al*. 2015; Giakoumi *et al*. 2018; Lomba *et al*. 2015; Sutcliffe *et al*. 2015).

Agricultural land-use changes contribute to biodiversity loss worldwide, including in regions where high species endemism and intensive agricultural use coincide (Kehoe *et al.* 2015). Agricultural intensification is a global process, in which extensive, marginally-viable agricultural systems transform into more efficient, modern systems. With past, present and predicted future increases in global food demands (Godfray *et al.* 2010; Tilman *et al.* 2011), the need for more efficient food-production systems increases, to ensure global food security (Tscharntke *et al*. 2012). The responses of European farmland birds to agricultural intensification have been well studied. There are several types of agricultural intensification processes that have been shown to contribute to biodiversity loss of birds and other taxa in European low-intensity agricultural landscapes. Pesticide use was linked with reduced abundance of habitat generalist birds in France (Chiron *et al*. 2014). In a

Europe-wide study it was found that the use of insecticides and fungicides had consistent negative effects on wild plant, carabid and farmland bird richness, and herbicide use had negative effects on wild plant richness (Geiger *et al*. 2010). Irrigation was found to severely effect open-habitat specialist bird species in a dry cereal agroecosystem in northwestern Spain increased mechanisation and irrigation (De Frutos, Olea, & Mateo-Tomás 2015). Loss of structural heterogeneity at different spatial scales might affect biodiversity too. Landscape simplification was associated with a loss of farmland bird species diversity in France (Chiron *et al*. 2014). In a study on farmland birds in France, diversity and community responses to landscape homogenisation were found to be scale-dependent (Jeliazkov *et al.* 2016). Compositional heterogeneity was positively linked with the richness of farmland and steppe birds in southern Portugal (Santana *et al.* 2017).

Grasslands cover about 30% of the Earth surface, and supply important ecological services to humans such as support for livestock grazing and its economic products, climate and weather amelioration and soil conservation (Sala & Paruelo 1997). Grassland systems managed for fodder crops and livestock are especially sensitive to land-use changes, due to their natural dependency on intermediate levels of disturbance (Collins & Glenn 1997; Shea, Roxburgh, & Rauschert 2004), and their attractiveness for conversion into cropland and other land-uses (Fargione *et al.* 2009; Sala & Paruelo 1997). Grassland systems have suffered considerably from land-use change processes, and are among the most altered ecosystems in the world, with 54.2% of their historical area lost (Heidenreich 2009; Hoekstra *et al.* 2005).

The area of grasslands in EU declined by 12.8% from 1990 to 2003 (Silva *et al.* 2008). As a result, grassland biodiversity in Europe is fast declining (Pe'er *et al.* 2014; van Swaay *et al.* 2015). Over millennia of agricultural land transformations in Europe, grassland biodiversity survived mainly in extensive agricultural systems (Donald, Green, & Heath 2001). Farmland birds include many grassland species, and are the fastest declining group of birds in Europe (Butler *et al.* 2010; Inger *et al.* 2015). The decline of European farmland birds has not been halted, despite considerable conservation and research efforts to preserve them through a network of targeted protected areas to conserve farmland birds and targeted agri-environmental schemes (Palacin & Alonso 2018; Silva *et al*. 2018; Gamero *et al.* 2017; Pe'er *et al*. 2014). Most bustard species survive in low-intensity agricultural systems, and not surprisingly 15 out of 26 bustard species are globally threatened (7 NT, 4 VU, 2 EN, 2 CR; BirdLife International 2017a). Long-term studies of Iberian farmland and grassland bird species are few (Palacín & Alonso, 2018; SEO/BirdLife, 2015). The reasons for their declines are not fully clear, and the conservation status of the agro-steppe bird assemblage that relies on anthropogenic extensive pastoral – cereal system, that contains several globally threatened species, need to be clarified. Understanding large-scale, long-term processes of both temporal trends of study species and land-use changes, may allow a unique and insightful approach to understand conservation implications and priorities. The implications for conservation of understanding the effects of agricultural land-use changes on population trends can be applied in other systems worldwide, especially in open, low-intensity agricultural systems that are often important for biodiversity conservation (Wright, Lake, & Dolman 2012).

1.2 Biodiversity conservation

With the biodiversity crisis described in section 1.1, the need to conserve biodiversity in the world has developed mainly in the 19th and early 20th century, as researchers started to understand and address factors related to biodiversity declines (Soulé 1985; Van Dyke 2008). Biodiversity conservation aims to manage management of natural resources for the purpose of sustaining biodiversity in species, ecosystems, and evolutionary processes (Bowen, 1999) and human culture and society (Chan et al., 2007). The developing science of conservation biology informed actions that were at first mainly directed towards protection of important areas for biodiversity (Butchart et al., 2012), and actions aimed directly at declining and threatened species (Maczulak, 2010). In recent decades, realising the effects of climate change on biodiversity (Araújo & Rahbek, 2012; Hampe & Petit, 2005), global conservation planning efforts include climate change considerations (Bellard*et al.* 2012; Groves *et al*. 2012). More holistic approaches, connecting between human population livelihoods and ecosystem services (Haines-Young & Potschin 2010) also drive global conservation efforts (Daily *et al*. 2009; Pressey *et al*. 2007; Sunderlin *et al*. 2005).

In the European Union, the main tools for conservation are nature and biodiversity laws (Birds Directives 2009/147/EC, Habitats Directive 92/43/EEC), species protection, development of knowledge and data webs, protection of key sites for biodiversity through NATURA 2000 network, and promotion of Green Infrastructure for sustainable development (source: http://ec.europa.eu/environment/nature/). In Europe, a focus in biodiversity conservation through declaration of PAs is on low-intensity agricultural landscapes,

where most European biodiversity has concentrated after millennia of human alterations of landscapes (Bignal & McCracken, 2000; Blondel, 2006; Klein Goldewijk *et al.* 2011). Despite these efforts to conserve biodiversity in low-intensity agricultural SPAs, terrestrial biodiversity, and especially farmland biodiversity, is still declining in Europe (Butler, Vickery, & Norris 2007; Pe'er *et al*. 2014). See Section 1.1 for explanation about causes of these declines. The effectiveness of SPAs in Europe to halt land-use changes is unclear. Europe's oldest PA were found to be effective in limiting the land use change within their boundaries between 1900 and 2000 (Camilo & Concha 2015). At the EU level, between 2000 and 2006 artificial surfaces and agricultural areas showed lower rates of transformation within PAs than outside (Kallimanis *et al*. 2015). However, in a network of agro-steppe SPAs in Spain and Portugal, area of agro-steppe habitats decreased in 10 SPAs between 2004-2006 and 2010-2013 by 5%, but greater losses were observed outside SPAs than inside SPAs (Gameiro 2015).

Identifying farmland biodiversity declines through monitoring and research, and understanding the causes of such declines, remains of high priority in European conservation (Gamero *et al*. 2017). Research and conservation of single species is still important, especially if they are regarded as surrogate species (EEA 2007; Gregory *et al*. 2005); this study contributes to this knowledge-base.

1.3 Wildlife monitoring for conservation

For decades, data on the distribution and abundance of wildlife have been used in conservation (Nichols & Williams 2006). While monitoring efforts were traditionally diverted towards threatened taxa (Campbell *et al.* 2002), in recent decades more monitoring attention is focused on monitoring of common taxa. Because funds for wildlife monitoring are always limited, wildlife monitoring for conservation constantly changes and revises methods to achieve efficiency, accuracy and effectiveness (Stem *et al.* 2005). Among the most important methods to reach efficiency, accuracy and effectiveness of monitoring are development of citizen-science systems (Conrad & Hilchey 2011; Dickinson, Zuckerberg, & Bonter 2010; Sullivan *et al.* 2014, 2017), the use of indicator, umbrella or surrogate species or groups of taxa to indicate wider biodiversity (Gilby *et al.* 2017; Lambeck 1997; Pakkala *et al.*, 2014; Simberloff 1998), and development of large-scale monitoring schemes that share and pool together knowledge and resources (Messer, Linthurst, & Overton 1991; Proença *et al.* 2017). In the EU, member states are obliged to monitor habitats and their biodiversity according to the relevant agreements and treaties (under e.g. Birds Directive 2009/147/EC, Habitats Directive 92/43/EEC). Such large-scale monitoring schemes provide data that inform habitat management (Nichols & Williams 2006; Perkins *et al.*2011), species conservation (Zimmerman *et al.*, 2015), hunting quotas (Molinari-Jobin *et al.* 2003; Otis 2006; Tautin, Metras, & Smith 1999) and more. Threatened taxa, as well as common taxa, and especially birds, are monitored in national programmes (Ram *et al.* 2017) or pan-continental monitoring schemes (Eaton *et al.* 2017; Heidenreich 2009; North American Bird Conservation Initiative 2007, 2017).

As funds are often limited, and monitoring cannot include entire ecosystems (Carignan & Villard 2002), wildlife monitoring for conservation is often limited to surrogate species: flagships, umbrella or indicators, which are assumed to represent the conservation status of a larger species assemblage, community or system (Carter, Resh & Hannaford, 2017; Hansson 2000; Osborne & Seddon 2012; Veríssimo *et al.* 2014).

The use of single species as indicators for wider biodiversity is still common practice in many cases, despite evidence showing variable effectiveness of the use of single-species indicators (Branton & Richardson 2011; Fleishman, Blair, & Murphy 2001; Gao, Nielsen, & Hedblom 2015; Heino 2010). Multi-taxa indices that incorporate several species (Lambeck 1997; Simberloff 1998), indigenous local knowledge combined with science (Ngo & Webb 2017), functional traits (Ricotta, Carboni, & Acosta 2015; Vandewalle *et al.* 2010) or niche-based lists of indicators (Butler *et al.* 2012; Wade *et al.* 2014) are used in increasing frequency to indicate the state of the wider environment.

Several types of single-species indices are used in conservation to indicate wider taxa, generally named surrogate species, including flagship, umbrella, indicator, and keystone species (Andelman & Fagan 2000; Caro & O'Doherty 1999). The distinction between these groups is not often clear, and they are occasionally used confusingly in different contexts (Armstrong & Caro 2002). Generally, surrogate species can be divided into three groups with some overlap: species used to locate areas of special environmental importance – Keystone, Indicator; species used to indicate environmental change in biological systems – Indicator, Umbrella;

and species, often iconic, used in to address public, farmers etc. – Flagship (Caro 2010). Despite their common deployment in conservation monitoring, evidence on the effectiveness of surrogate species as indicators of wider biodiversity is still limited, especially for unique species with extraordinary life cycles which, because of their broader habitat needs, may include more taxa 'under their umbrella'.

Monitoring single species and single populations is still important, especially if those species are threatened and/or declining. According to EU regulations manifested in the Birds Directive, EU members are obliged to monitor Great Bustards in their area. Monitoring Great Bustards is also important because of its possible function as a flagship species for conservation of agro-steppe bird species, or an indicator for the conservation status of those species (see Section 1.4 for explanations of these terms). Currently, there is no formal definition of Great Bustard as an indicator or flagship species in Iberia, but in practice it is used as a flagship species to promote public activity in at least Castro Verde in Alentejo (see Fig. 1.2), and in ZEPA Llanos de Cáceres y Sierra de Fuentes in Extremadura (Agustín Mogena, pers. comm.). It is important to monitor Great Bustards in the regional concentration in Extremadura and Alentejo, because it holds a substantial proportion of the total numbers in Iberia (see Chapter 2), because of its possible use as a study species to investigate links between population trends and land-use changes (see Chapter 3) and because of its possible use as an indicator species for agro-steppe birds (see Chapter 4). In threatened species, the study of demographic mechanisms that drive population changes is important too (see Chapter 5).

Figure 1.2: Entrance to the village Sao Marcos de Ataboeira in Castro Verde, Alentejo. Photo by Yoav Perlman.

1.4 Monitoring the effectiveness of Protected Areas

Currently, 15% of Earth is designated as some form of 'Protected Area' (PA) (Fig. 1.3; UNEP-WCMC and IUCN 2016). In Europe, 21% of European Economic Area were protected in 2012 (European Environment Agency 2012). Natura 2000 network is a network of protected area designated to ensure the long-term survival of Europe's most valuable and threatened species and habitats, listed under both the Birds Directive and the Habitats Directive of the European Union. This network covers 787,606 km^2 that are 18% of Europe's land area, and 360,350 km^2 that are 6% of its marine area (Kati *et al.* 2015). Natura 2000 network was founded upon the Birds Directive (Council Directive 2009/147/EC on the conservation of wild birds) first adopted in 1979, that protects the most important sites for birds (Special Protection Areas, SPAs), and the Habitats Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora) adopted in 1992, that protects the most important sites for organisms that are not birds, and for habitats, especially particular types of forests, grasslands and wetlands (Special Areas for Conservation, SACs). SPAs are designated directly by each EU member state, while SACs are designated through more elaborate process that includes approval by the European Commission. In the USA, 12.9% of land area and 41% of marine area are protected (UNEP-WCMC 2018). Most federally protected land is part of the National Park Service network, along with United States Forest Service, Bureau of Land Management and United States Fish and Wildlife Service (PAD-US Partnership 2009).

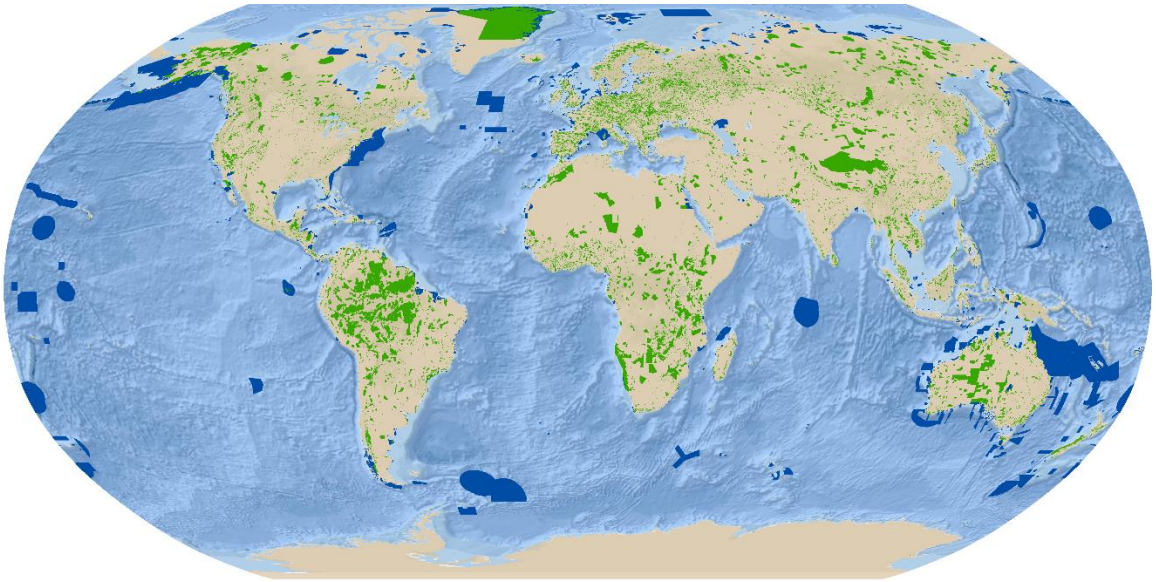


Figure 1.3: Protected areas of the world. Green are terrestrial protected area. Blue are marine protected areas. Source: IUCN and UNEP-WCMC (2016). The World Database of Protected Areas (WDPA) [On-line], April 2016, Cambridge, UK: UNEP-WCMC, Available at www.protectedplanet.net

Evaluating the effectiveness of protected areas in conserving biodiversity is a challenging task, because of the need for suitable indicator species (Timko & Innes 2009), the need for long-term, large-scale data, and the necessary comparison with similar habitats outside protected areas that are often lacking. Most studies that have evaluated the effectiveness of protected areas focus on single species or single sites (e.g. Palacín & Alonso 2018; Santana *et al.* 2014; Silva *et al.* 2018). Large-scale studies that have evaluated the effectiveness of networks of protected areas in protecting biodiversity directly, and not through habitat indices such as forest cover or land-use change (Bruner *et al.* 2001; Figueroa & Sánchez-Cordero 2008), are rather few, and have not been wholly positive (Ferraro & Pattanayak 2006; Kleijn *et al.* 2006; Leverington *et al.* 2010; Parrish, Braun, & Unnasch 2003). In northern Italy, the effects of agri-environmental schemes in protected areas were

found to be very limited and not all positive (Calvi *et al*. 2018). In Spain and Portugal, protected areas reasonabely represented 73-98% of plant and animal species considered in this study, but amphibians, birds, reptiles and gymnosperms were not found in protected areas at a rate higher than expected by chance (Araújo, Lobo, & Moreno 2007). A network of protected areas in Portugal did not halt declines of Little Bustards (*Tetrax tetrax*) (Silva *et al*. 2018). In a protected area in central Spain, trends of four agro-steppe birds of conservation concern were negative (Palacín & Alonso 2018). In southern Portugal, mixed effects of conservation investment in a NATURA 2000 protected area were found: while several priority and specialised fallow species fared better inside the protected area compared to outside, the opposite was found for total bird species, farmland, ground-nesting and steppe species, species associated to ploughed fields, and species of European conservation concern (Santana *et al*. 2014). Certainly, further large-scale studies of the Natura 2000 network are necessary to determine ways to improve its ambiguous effectiveness for biodiversity conservation using agri-environmental schemes as the main tool (Pe'er *et al.* 2014).

There is a gap in knowledge about the effectiveness of the network of NATURA 2000 agro-steppe SPAs for the protection of Great Bustard and other agro-steppe bird species. This study contributes to fill this gap of knowledge.

1.5 The Great Bustard

The Great Bustard (*Otis tarda*) is used as a study species in my research. In this section I outline its relevant life history attributes and its conservation worldwide, especially in the context of its vulnerability to modern agricultural developments.

The Great Bustard is the heaviest flying bird in Europe. It demonstrates the most extreme sexual dimorphism among birds (Alonso *et al*. 2009). Body size of the male is 90-105 cm and weight is 5.8-18 kg; female body size is 75-85 cm and weight is 3.3-3.5 kg (Collar & Garcia, 2018). As a result of this extreme sexual dimorphism, both sexes are potentially exposed to different conservation threats. Size differences between the sexes are apparent from an early stage. Males, because of their size, experience higher mortality rates than females already in their first months of life. The male chick's faster growth rate (Quaisser *et al*. 1998 in: Martín *et al*. 2007) and higher vulnerability to reduced food availability at early stages was suggested as a reason for sexually-differential juvenile mortality rates (Martín *et al*. 2007). In adulthood, male mortality is again higher than female mortality, possibly as a result of their high collision rates with powerlines (Palacín *et al*. 2016). These sexual differences in mortality rates lead to uneven sex ratios in Great Bustard populations. A biased sex-ratio is expected even is stable populations, as observed in Castro Verde in southern Portugal, where sex ratio was reported to be 1 male : 1.26 female (Morgado & Moreira 2000). In declining populations, an even stronger bias in sex-ratio can be expected (Donald 2007), as demonstrated in the threatened population in Andalusia, where a highly biased sex ratio of 1 male : 3.28 females was reported (Alonso *et al.* 2005). Interestingly, in the rapidly declining population in Saratov, Russia, sex ratio was 1.08 males to 1 female (Oparin *et al*. 2013).

Great Bustards use a lekking mating system, in which males congregate to perform display communally in display arenas, sometimes several tens of males together, and they take no part in parental care (Alonso, Álvarez-Martínez & Palacín 2012; Morales, Jiguet & Arroyo 2001). Great Bustards use a non-classical lekking system called 'Exploded Lek', in which concentration of males is detectable only across a large spatial scale (Morales, Jiguet & Arroyo 2001). Lekking typically takes place in late March to early April. Females concentrate in the lek, in which they copulate with their chosen male, often a dominant male; dominance is determined by age, weight and display effort (Alonso *et al*. 2010). Females may travel considerable distances to mate in a lek. In central Spain, nest locations of 55% of tagged females were <5 km from leks, and mean nest-to-lek distance was 7.73 km (range 0.22–53.82 km, SD = 9.49, n = 55 birds) (Magaña *et al.* 2011). After breeding, typically in mid-May – early-June, males leave the lek and disperse towards their non-breeding grounds (Palacín *et al*, 2009).

Great Bustard breeding performance and productivity has been studied in several parts of Iberia. In Alentejo, mean clutch size was 2.12 (SD=0.69, n=86); overall nesting success was 71% (n=107) (Rocha, Morales, & Moreira 2012). In northwestern Spain, overall productivity was low, with 0.14 chicks reared per adult females (c. 700 adult females), and high inter-annual variability among a sample of 32 marked females (mean=0.15, range 0.04-0.29). Productivity was found to be positively correlated with winter precipitation prior to each breeding season (Morales, Alonso, & Alonso 2002). In a later study in northwestern Spain, mean productivity was 0.24 (SD=0.35, 0-3) (Martínez 2008).

Great Bustard is a partial migrant in Iberia and in central Europe (Alonso, Morales, & Alonso, 2000; Streich *et al.*, 2006), while it is an obligate migrant farther east in its range in Russia and China (Kessler *et al.* 2013; Oparin, Kondratenkov, & Oparina 2003). In Iberia, while both males and females show high fidelity to their nesting areas during the breeding season (Alonso *et al.* 2001; Palacín *et al*. 2009), sexes differ in their tendency and consistency of non-breeding migrations: females are more sedentary and more consistent in their partial migration strategies than males: In central Spain, 86% of males carried out post-breeding migration, while only 51% of females did so; males migrated to a mean of 109.4 km, females to 49.8 km (Palacín *et al*. 2009; Palacín *et al*. 2011). Iberian males have a capacity for medium length migration, and have been recorded migrating up to 172 km between lek site and non-breeding site (Palacín *et al*. 2009). Therefore, males in Iberia are more exposed to risks along their migration routes and on their non-breeding grounds comparted to females (Palacín *et al*. 2016). Extreme site fidelity during the breeding season may also expose both sexes to higher risks when habitat is lost or degraded, as they will often not leave their original breeding sites to occupy suitable and available patches of habitat (Lane, Alonso, & Martín 2001; Osborne, Alonso, & Bryant 2001).

Great Bustards typically utilise flat or undulating grasslands and anthropogenic low-intensity agricultural landscapes. They have been found to select various components of traditional cereal-pastoral agricultural systems: fallows, stubbles, cereals and pastures (Alonso, Álvarez-Martínez, & Palacín 2012; Lane, Alonso, & Martín 2001; Lopez-Jamar *et al.*, 2010; Magaña *et al*. 2010; Rocha, Morales, & Moreira 2012; Schwandner & Langgemach 2011), which in Iberia are

components of the three- or four-year cereal-pastoral rotational system (Caballero *et al*. 2009; Suárez, Naveso, & De Juana 1997).

Some sexual differences were found in habitat selection during the breeding season, affected by their lekking mating system in which males congregate in display arenas (Morales et al., 2001). Males require good visibility from their elevated lek sites, often provided by short grass (Alonso *et al*. 2012). Females leave the lek after copulating to breed in tall-grass fallows and cereal fields (Rocha, Morales, & Moreira 2012) with good horizontal visibility, suggesting a trade-off in nest location selection between concealment and visibility (Magaña *et al*. 2010).

Great Bustards are exposed to several anthropogenic threats. Agricultural intensification has long been suggested as a cause of population declines (Alonso *et al.* 2000; Lane & Alonso 2001; Oparin *et al*. 2013; Pinto, Rocha, & Moreira 2005; Raab *et al*. 2010; Sánchez & Garcia - Baquero 2012) but this proposition, while of course entirely plausible, has not been formally tested. Other anthropogenic causes of direct mortality have been better documented. Collision with powerlines is one major cause of mortality (Palacín *et al*. 2016; Raab *et al*. 2014; Vadász & Lóránt 2014). Nest destruction by farming machinery is another threat, primarily involving eggs and chicks in hay fields and early-harvested crops, although females can also be killed (Faria, Morales, & Rabaça 2016; Rocha *et al*. 2012; Vadász & Lóránt 2014). Until the 1980's, hunting was a major cause of mortality, but hunting seems to have been largely eliminated in Iberia as a result of legislation (Alonso 2014), although it may still occur in less-regulated regions (Karakaş & Akarsu 2009).

Great Bustard is a globally Vulnerable species which occupies open, relatively flat landscapes from Morocco and Portugal in the west of its range to the far eastern regions of Russia and China (BirdLife International 2018). Global numbers increased in the 1990's and 2000's to 44,100–57,000 (Alonso & Palacín 2010), and have been considered to be currently stable (Alonso 2014). Despite its overall population stability, it is still threatened and its numbers have been reported to be in decline also in European Russia (Oparin *et al*. 2013), and in Morocco, Iran and Turkey (in Alonso 2014).

In Europe, the population size was last estimated in Alonso (2014) at 41,754-50,917. The largest proportion of the global population (60-70%) is found in Iberia (Alonso & Palacín 2010). However, current numbers in Europe might be reduced as a result of ongoing declines in European Russia, reported at a rate of 70% compared to the late 1990's (Oparin *et al*. 2013). It is possible that numbers in Iberia are declining in recent years, with potentially worrying reports of declines in Extremadura, down from 5,500 – 6,500 in 2003 (Alonso *et al*. 2005) to 2,319 in 2015 (Chapter 2), and an annual decrease of 1% in an SPA in central Spain, Estepas cerealistas de los Ríos Jarama y Henares (Palacín & Alonso 2018).

Great Bustard conservation efforts globally have had mixed success. Such efforts include habitat protection, and captive breeding and reintroduction. Ban on hunting was introduced in most of its range in the 1980's (Alonso 2014). West-Pannonian Great Bustards have experienced dramatic declines from at least 3,500 individuals in 1900 to 130 in 1995, as a result of agricultural transformations, development of human infrastructure and hunting pressure. Recently, numbers

there increased to 400 birds in 2013 through the establishment of cross-border protected areas, habitat management and burying of powerlines (Faragó, Spakovszky, & Raab 2014; Raab *et al.* 2010). In Germany, numbers dropped from ca. 4,000 in 1940 to 55 in 1995. Conservation efforts that included habitat protection and captive breeding program prevented the extinction of the German population, and currently numbers recovered slightly to 165 in 2014 (information available from http://www.grosstrape.de). After becoming extinct in the UK during the 19th century due to hunting, egg collection and changes in agriculture, intensive reintroduction efforts from the 2000's have resulted in partial success and first breeding (Burnside *et al.* 2012). In Russia, captive breeding efforts and nest protection have been so far unsuccessful (in Alonso 2014), as manifested by the dramatic population declines there (Oparin *et al*. 2013). In Hungary, numbers dropped from 3,000 in the mid 20th century to 1,200 in 2008, as a result of agricultural changes and habitat loss (information available from www.tuzok.hu). In recent years, conservation efforts that included habitat management towards extensive agricultural practices, predator control and captive breeding, have increased numbers to 1,466 in 2014 (in Alonso 2014). In Villafáfila Lagoons Reserve in Castilla y León in northwesten Spain, heavy investment in agri-environmental schemes, manifested mainly in expansion of alfalfa growing targeted at Great Bustards, has had positive effects on the numbers there, with a 34% increase from 1998 to 2008, up to 14,025 birds (Martín *et al.* 2012). In southern Portugal, effective implementation of agri-environmental schemes has resulted in a steady increase of numbers in Castro Verde, which is now the national stronghold of the

species and one of the most important sites in Iberia (Pinto *et al*. 2005; Santana *et al*. 2014).

In the study area of this research, Extremadura and Alentejo, an important proportion of the Iberian population is found. However, estimates for Iberia require update. In Extremadura (updated for 2005, based on data from 2002–2003: Corbacho *et al.* 2005) and Alentejo (updated for 2009: Alonso & Palacín 2010) comprise 20–27% of the estimated total Iberian population of 31,293–36,193 (Alonso & Palacín 2010). Bringing into account the results found in Chapter 2, with somewhat outdated estimates of the total Iberian population (Alonso & Palacín 2010), the proportion found in the study area drops down to 9.7 – 11.2%.

To conclude, Great Bustard is vulnerable to modern development, because of its dependency on low-intensity agriculture, and its high risk of mortality from anthropogenic structures, especially powerlines. Despite deep research on the biology and ecology of Great Bustard, it is still threatened and apparently declining. Gaps in knowledge about the causes of declines prevent effective conservation, and need to be addressed.

1.6 Research aims

This study aims to fill gaps in our knowledge on conservation of Great Bustards and other open country birds in the agro-steppe systems of Extremadura (Spain) and Alentejo (Portugal), on the use of indicator species in biodiversity monitoring, and on the function of the agro-steppe Natura 2000 network across Extremadura and Alentejo to protect threatened grassland and farmland birds.

Using long-term large-scale Great Bustard monitoring data from Extremadura and Alentejo, I described temporal trends of demographic units (subpopulations) and searched for regional patterns among those trends (Chapter 2).

Assuming that agricultural land-use changes have had an important impact on Great Bustard subpopulation trends, I aimed to link those trends with agricultural land-use changes, using open-access land-cover and agricultural databases, to explain the trends identified in Chapter 2 (Chapter 3).

Great Bustard is used as a surrogate for other agro-steppe bird species across a network of agro-steppe Natura 2000 protected areas. I aimed to understand whether sites that are good for Great Bustards are good also for other agro-steppe bird species, by linking counts of bird species that belong to that species assemblage with Great Bustard counts, inside protected areas and outside them (Chapter 4).

In my final data chapter, I used an exceptional dataset of productivity counts of Great Bustards from their stronghold in Extremadura. I aimed to understand whether Great Bustard productivity at this site is decreasing, and to use current

demographic rates to predict what the trend of the Great Bustard population will be at this stronghold in the future (Chapter 5).

Finally, I acknowledge the key findings of this study, discuss their potential importance for conservation and applications for management of protected areas for agro-steppe birds in Extremadura and Alentejo, and propose future research directions (Chapter 6).

1.7 Author contributions

Chapter 2 in its current form is a result of extensive joint work with my supervisors towards submission of the chapter as a manuscript to a journal. In the process of the manuscript preparation, deep editing was carried out by my supervisors, especially by Nigel Collar. Chapter 2 was submitted as a manuscript to Oryx, and was returned with reviews and an invitation to resubmit. In further data chapters, and more so in Chapter 3, all supervisors contributed advice and editing in various iterations and drafts.

1.8 References

Alonso, J. A., Martín, C. A., Alonso, J. C., Morales, M. B., & Lane, S. J. (2001). Seasonal movements of male great bustards in central Spain. *Journal of Field Ornithology*, **72**, 504–508.

Alonso, J. C. (2014). The great bustard: Past, present and future of a globally threatened species. *Ornis Hungarica*, **22**, 1–13. doi:10.2478/orhu-2014-0014

Alonso, J. C., Álvarez-Martínez, J. M., & Palacín, C. (2012). Leks in ground-displaying birds: hotspots or safe places? *Behavioral Ecology*, **23**, 491–501.

Alonso, J. C., Magaña, M., Palacín, C., & Martín, C. A. (2010). Correlates of male mating success in great bustard leks: The effects of age, weight, and display effort. *Behavioral Ecology and Sociobiology*, **64**, 1589–1600. doi:10.1007/s00265-010-0972-6

Alonso, J. C., Martín, C. A., Palacín, C., Martín, B., & Magaña, M. (2005). The great bustard *Otis tarda* in Andalusia, southern Spain: Status, distribution and trends. *Ardeola*, **52**, 67–78.

Alonso, J. C., Lane, S. J., Dawson, R., & Idaghdour, Y. (2000). Great bustards *Otis tarda* in Morocco: Status in spring 1999 and evidence of a decline in recent decades. *Oryx*, **34**, 141–146.

Alonso, J. C., Magaña, M., Alonso, J. A., Palacín, C., Martín, C. A., & Martín, B. (2009). The most extreme sexual size dimorphism among birds: allometry, selection, and early juvenile development in the great bustard (*Otis tarda*). *Auk*, **126**, 657–665. doi:10.1525/auk.2009.08233

Alonso, J. C., Morales, M. B., & Alonso, J. A. (2000). Partial migration, and lek and nesting area fidelity in female great bustards. *Condor*, **102**, 127–136.

Alonso, J. C., & Palacín, C. (2010). The world status and population trends of the great bustard (*Otis tarda*): 2010 update. *Chinese Birds*, **1**, 141–147. doi:10.5122/cbirds.2010.0007

Andelman and Fagan, W. F., S. J. (2000). Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 5954–5959.

Araújo, M. B., & Rahbek, C. (2012). How does climate change affect biodiversity? *Science*,

1396, 1396–1398. doi:10.1126/science.1131758

Araújo, M. B., Lobo, J. M., & Moreno, J. C. (2007). The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. *Conservation Biology*, **21**, 1423–1432. doi:10.1111/j.1523-1739.2007.00827.x

Armstrong, D., & Caro, T. (2002). Focal and surrogate species: Getting the language right. *Conservation Biology*, **16**, 285–287.

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, **29**, 1006–1016. doi:10.1111/cobi.12536

Beketov, M. A., Kefford, B. J., Schäfer, R. B., & Liess, M. (2013). Pesticides reduce regional biodiversity of stream invertebrates. Proceedings of the National Academy of Sciences, **110**, 11039–11043. doi:10.1073/pnas.1305618110

Bellard, C., Bertelmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2014). Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377. doi:10.1111/j.1461-0248.2011.01736.x.Impacts

Bignal, E. M., & McCracken, D. I. (2000). The nature conservation value of European traditional farming systems. *Environmental Reviews*, **8**, 149–171. doi:10.1139/er-8-3-149

BirdLife International. (2018). Species factsheet: *Otis tarda*. Retrieved from http://www.birdlife.org/datazone/

Blondel, J. (2006). The “design” of Mediterranean landscapes: A millennial story of humans and ecological systems during the historic period. *Human Ecology*, **34,** 713–729. doi:10.1007/s10745-006-9030-4

Bowen, B. W. (1999). Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. *Molecular Ecology*, **8**, S5–S10. doi:10.1046/j.1365-294X.1999.00798.x

Branton, M., & Richardson, J. S. (2011). Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. *Conservation Biology*, **25**, 9–20. doi:10.1111/j.1523-1739.2010.01606.x

Bruner, A. G., Gullison, R. E., Rice, R. E., & da Fonseca, G. A. B. (2001). Effectiveness of parks

in portecting tropical biodiversity. *Science*, **291**, 125–128. doi:10.1126/science.291.5501.125

Burnside, R. J., Carter, I., Dawes, A., Waters, D., Lock, L., Goriup, P., & Szekely, T. (2012). The UK great bustard *Otis tarda* reintroduction trial: A 5-year progress report. *Oryx*, **46**, 112–121. doi:10.1017/s0030605311000627

Butchart, S. H. M., Scharlemann, J. P. W., Evans, M. I., Quader, S., Aricò, S., Arinaitwe, J., … Woodley, S. (2012). Protecting important sites for biodiversity contributes to meeting global conservation targets. *PLoS ONE*, **7**, 1–8. doi:10.1371/journal.pone.0032529

Butler, S. J., Vickery, J. A., & Norris, K. (2007). Farmland biodiversity and the footprint of agriculture. *Science*, **315**, 111–116.

Butler, S. J., Boccaccio, L., Gregory, R. D., Vorisek, P., & Norris, K. (2010). Quantifying the impact of land-use change to European farmland bird populations. *Agriculture, Ecosystems and Environment*, **137**, 348–357. doi:10.1016/j.agee.2010.03.005

Butler, S. J., Freckleton, R. P., Renwick, A. R., & Norris, K. (2012). An objective, niche-based approach to indicator species selection. *Methods in Ecology and Evolution*, **3**, 317–326. doi:10.1111/j.2041-210X.2011.00173.x

Caballero, R., Fernández-gonzález, F., Badia, R. P., Molle, G., Roggero, P. P., Bagella, S., … Ispikoudis, I. (2009). Grazing Systems and Biodiversity in Mediterranean Areas: Spain, Italy and Greece. *Pastos*, **39**, 9–152. doi:10.1111/j.1365-2494.2011.00820.x

Camilo, I., & Concha, V. (2015). Assessing land use change in Europe's protected areas through time. *Revista de Tecnología*, **14**, 7-22.

Campbell, S. P., Clark, J. A., Crampton, L. H., Guerry, A. D., Hatch, L. T., Hosseini, P. R., … O'Connor, R. J. (2002). An assessment of monitoring efforts in endangered species recovery plans. *Ecological Applications*, **12**, 674–681. Retrieved from http://www.jstor.org/stable/3060977

Calvi, G., Campedelli, T., Tellini Florenzano, G., & Rossi, P. (2018). Evaluating the benefits of agri-environment schemes on farmland bird communities through a common species monitoring programme. A case study in northern Italy. *Agricultural Systems*, **160**, 60–69. doi:10.1016/j.agsy.2017.09.002

Carignan, V., & Villard, M.-A. (2002). Selecting indicator species to monitor ecological integrity: A review. *Environmental Monitoring and Assessment*, **78**, 45–61.

doi:10.1023/A:1016136723584

Caro, T. (2010). *Conservation by Proxy: Indicator, umbrella, keystone, flagship and other surrogate species*. Washington DC: Island Press.

Caro, T. M., & O'Doherty, G. (1999). On the use of surrogate species in conservation biology. *Conservation Biology*, **13**, 805–814.

Carter, J. L., Resh, V. H., & Hannaford, M. J. (2017). Macroinvertebrates as biotic indicators of environmental quality. In G. A. Lamberti & F. R. Hauer (Eds.), *Methods in Stream Ecology* (3rd ed., pp. 293–318). Elsevier. doi:10.1016/B978-0-12-813047-6.00016-4

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., Garcia, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, **1**, 1–5. doi:10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, **114**, 1–8. doi:10.1073/pnas.1704949114

Chan, K. M. A., Pringle, R. M., Ranganathan, J., Boggs, C. L., Chan, Y. L., Ehrlich, P. R., … Macmynowski, D. P. (2007). When agendas collide: Human welfare and biological conservation. *Conservation Biology*, **21**, 59–68. doi:10.1111/j.1523-1739.2006.00570.x

Chiron, F., Chargé, R., Julliard, R., Jiguet, F., & Muratet, A. (2014). Pesticide doses, landscape structure and their relative effects on farmland birds. *Agriculture, Ecosystems and Environment*, **185**, 153–160. doi:10.1016/j.agee.2013.12.013

Collar, N., & Garcia, E. F. J. (2018). Great Bustard (*Otis tarda*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions. Retrieved from https://www.hbw.com/node/53712

Collins, S. L., & Glenn, S. M. (1997). Intermediate disturbance and its relationship to within and between patch dynamics. *New Zealand Journal of Ecology*, **21**, 103–110.

Conrad, C. C., & Hilchey, K. G. (2011). A review of citizen science and community-based environmental monitoring: Issues and opportunities. *Environmental Monitoring and Assessment*, **176**, 273–291. doi:10.1007/s10661-010-1582-5

Daily, G. C., Polasky, S., Goldstein, J., Kareiva, P. M., Mooney, H. A., Pejchar, L., … Shallenberger, R. (2009). Ecosystem services in decision making: Time to deliver.

Frontiers in Ecology and the Environment, **7**, 21–28. doi:10.1890/080025

De Frutos, A., Olea, P. P., & Mateo-Tomás, P. (2015). Responses of medium- and large-sized bird diversity to irrigation in dry cereal agroecosystems across spatial scales. *Agriculture, Ecosystems and Environment*, **207**, 141–152. doi:10.1016/j.agee.2015.04.009

De Juana, E. (2009). The dramatic decline of the little bustard *Tetrax tetrax* in Extremadura (Spain). *Ardeola*, *56*, 119–125.

Dickinson, J. L., Zuckerberg, B., & Bonter, D. N. (2010). Citizen science as an ecological research tool: Challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 149–172. doi:10.1146/annurev-ecolsys-102209-144636

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, *113*, 11261–11265. doi:10.1073/pnas.1602480113

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 25–29. doi:10.1098/rspb.2000.1325

Donald, P. F. (2004). Biodiversity impacts of some agricultural commodity systems. *Conservation Biology*, *18*, 17–37.

Donald, P. F. (2007). Adult sex ratios in wild bird populations. *Ibis*, **149**, 671–692. doi:10.1111/j.1474-919X.2007.00724.x

Eaton, M. ., Frost, T., Grice, P. ., Hariis, S. ., Harvey, S., Hearn, R. ., … Wotton, S. (2017). *The state of the UK's birds 2017*. British Trust for Ornithology, Thetford. Retrieved from https://www.bto.org/file/344157/download?token=OR0lQe8r

EEA. (2007). *Halting the loss of biodiversity by 2010: proposal for a first set of indicators to monitor progress in Europe*.

Elmhagen, B., Destouni, G., Angerbjörn, A., Borgström, S., Boyd, E., Cousins, S. A. O., … Lindborg, R. (2015). Interacting effects of change in climate, human population, land use, and water use on biodiversity and ecosystem services. *Ecology and Society*, **20**, 23. doi:10.5751/ES-07145-200123

European Environment Agency (2007). *Halting the loss of biodiversity by 2010: proposal for*

a first set of indicators to monitor progress in Europe. Technical report, EEA.

European Environment Agency (2012). *Protected areas in Europe — an overview*. European Environment Agency, Copenhagen. doi:/10.2800/55955

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419

Faragó, S., Spakovszky, P., & Raab, R. (2014). Conservation of Great Bustard (*Otis tarda*) population of the Mosoni-Plain - a success story. *Ornis Hungarica*, **22**, 14–31. doi:10.2478/orhu-2014-0015

Fargione, J. E., Cooper, T. R., Flaspohler, D. J., Hill, J., Lehman, C., Tilman, D., … Oberhauser, K. S. (2009). Bioenergy and wildlife: Threats and opportunities for grassland conservation. *BioScience*, **59**, 767–777. doi:10.1525/bio.2009.59.9.8

Faria, N., Morales, M. B., & Rabaça, J. E. (2016). Exploring nest destruction and bird mortality in mown Mediterranean dry grasslands: an increasing threat to grassland bird conservation. *European Journal of Wildlife Research*, **62**. doi:10.1007/s10344-016-1039-4

Ferraro, P. J., & Pattanayak, S. K. (2006). Money for nothing? A call for empirical evaluation of biodiversity conservation investments. *PLoS Biology*, **4**, 482–488. doi:10.1371/journal.pbio.0040105

Figueroa, F., & Sánchez-Cordero, V. (2008). Effectiveness of natural protected areas to prevent land use and land cover change in Mexico. *Biodiversity and Conservation*, **17**, 3223–3240. doi:10.1007/s10531-008-9423-3

Fleishman, E., Blair, R. B., & Murphy, D. D. (2001). Empirical validation of a method for umbrella species selection. *Ecological Applications*, **11**, 1489–1501.

Foley, J. A., Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., … Snyder, P. K. (2005). Global consequences of land use. *Science*, **309**, 570–574. doi:10.1126/science.1111772

Gameiro, J. M. C. (2015). *Alterações de habitat: evolução das estepes cerealíferas em áreas protegidas do sudoeste da Península Ibérica*. Universidade de Lisboa.

Gamero, A., Brotons, L., Brunner, A., Foppen, R., Fornasari, L., Gregory, R. D., … Voříšek, P.

(2017). Tracking progress toward EU biodiversity strategy targets: EU policy effects in preserving its common farmland birds. *Conservation Letters*, **10**, 394–401. doi:10.1111/conl.12292

Gao, T., Nielsen, A. B., & Hedblom, M. (2015). Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators*, **57**, 420–434. doi:10.1016/j.ecolind.2015.05.028

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B., … Inchausti, P. (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, **11**, 97–105. doi:10.1016/j.baae.2009.12.001

Geiger, F., de Snoo, G. R., Berendse, F., Guerrero, I., Morales, M. B., Oñate, J. J., … Tscharntke, T. (2010). Landscape composition influences farm management effects on farmland birds in winter: A pan-European approach. *Agriculture, Ecosystems & Environment*, **139**, 571–577. doi:10.1016/j.agee.2010.09.018

Giakoumi, S., Hermoso, V., Carvalho, S. B., Markantonatou, V., Dagys, M., Iwamura, T., … Vogiatzakis, I. N. (2018). Conserving European biodiversity across realms. *Conservation Letters*, **11**, e12586. doi:10.1111/conl.12586

Gilby, B. L., Olds, A. D., Connolly, R. M., Yabsley, N. A., Maxwell, P. S., Tibbetts, I. R., … Schlacher, T. A. (2017). Umbrellas can work under water: Using threatened species as indicator and management surrogates can improve coastal conservation. *Estuarine, Coastal and Shelf Science*, **199**, 132–140. doi:10.1016/j.ecss.2017.10.003

Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., … Toulmin, C. (2010). Food security: The challenge of feeding 9 billion people. *Science*, *327*, 812–818. doi:10.1126/science.1185383

Gregory, R. D., Noble, D., Field, R., Marchant, J., Raven, M., & Gibbons, D. W. (2003). Using birds as indicators of biodiversity. *Ornis Hungarica*, **12**, 11–24.

Gregory, R. D., van Strien, A., Vorisek, P., Gmelig Meyling, A. W., Noble, D. G., Foppen, R. P. B., & Gibbons, D. W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *360*, 269–288. doi:10.1098/rstb.2004.1602

Groves, C. R., Game, E. T., Anderson, M. G., Cross, M., Enquist, C., Ferdaña, Z., … Shafer, S.

L. (2012). Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation*, **21**, 1651–1671. doi:10.1007/s10531-012-0269-3

Haines-Young, R. H., & Potschin, M. B. (2010). The links between biodiversity, ecosystem services and human well-being. In D. Raffaelli & C. Frid (Eds.), *Ecosystems Ecology: A New Synthesis*. Cambridge University Press. doi:10.1017/CBO9780511750458

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, **8**, 461–467. doi:10.1111/j.1461-0248.2005.00739.x

Hanski, I. (2011). Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *Ambio*, **40**, 248–255. doi:10.1007/s13280-011-0147-3

Hansson, L. (2000). *Indicators of biodiversity: recent approaches and some general suggestions*. Technical report for Swedish Environmental Protection Agency, Stockholm.

Heidenreich, B. (2009). *What are global temperate grasslands worth? A case for their protection. A review of current research on their total economic value*. Report prepared for The World Temperate Grasslands Conservation Initiative, Vancouver.

Heino, J. (2010). Are indicator groups and cross-taxon congruence useful for predicting biodiversity in aquatic ecosystems? *Ecological Indicators*, **10**, 112–117. doi:10.1016/j.ecolind.2009.04.013

Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters*, **8**, 23–29. doi:10.1111/j.1461-0248.2004.00686.x

Inger, R., Gregory, R., Duffy, J. P., Stott, I., Voříšek, P., & Gaston, K. J. (2015). Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters*, **18**, 28–36. doi:10.1111/ele.12387

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., … Larigauderie, A. (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, **546**, 65–72. doi:10.1038/nature22899

IUCN, U.-W. and. (2016). *Protected Planet Report 2016*. UNEP-WCMC and IUCN, Cambridge, UK. doi:/10.1017/S0954102007000077

Jeliazkov, A., Mimet, A., Chargé, R., Jiguet, F., Devictor, V., & Chiron, F. (2016). Impacts of

agricultural intensification on bird communities: New insights from a multi-level and multi-facet approach of biodiversity. *Agriculture, Ecosystems and Environment*, **216**, 9–22. doi:10.1016/j.agee.2015.09.017

Kallimanis, A. S., Touloumis, K., Tzanopoulos, J., Mazaris, A. D., Apostolopoulou, E., Stefanidou, S., … Pantis, J. D. (2015). Vegetation coverage change in the EU: patterns inside and outside Natura 2000 protected areas. *Biodiversity and Conservation*, **24**, 579–591. doi:10.1007/s10531-014-0837-9

Karakaş, R., & Akarsu, F. (2009). Recent status and distribution of the Great Bustard, *Otis tarda*, in Turkey. *Zoology in the Middle East*, **48**, 25–34. doi:10.1080/09397140.2009.10638363

Kati, V., Hovardas, T., Dieterich, M., Ibisch, P. L., Mihok, B., & Selva, N. (2015). The challenge of implementing the European network of protected areas Natura 2000. *Conservation Biology*, **29**, 260–270. doi:10.1111/cobi.12366

Kehoe, L., Kuemmerle, T., Meyer, C., Levers, C., Václavík, T., & Kreft, H. (2015). Global patterns of agricultural land-use intensity and vertebrate diversity. *Diversity and Distributions*, **21**, 1308–1318. doi:10.1111/ddi.12359

Kessler, A. E., Batbayar, N., Natsagdorj, T., Batsuur', D., & Smith, A. T. (2013). Satellite telemetry reveals long-distance migration in the Asian great bustard *Otis tarda dybowskii*. *Journal of Avian Biology*, **44**, 311–320. doi:10.1111/j.1600-048X.2013.00072.x

Kleijn, D., Baquero, R. A., Clough, Y., Díaz, M., DeEsteban, J., Fernández, F., … Yela, J. L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243–254.

Klein Goldewijk, K., Beusen, A., van Drecht, G., & de Vos, M. (2011). The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography*, **20**, 73–86. doi:10.1111/j.1466-8238.2010.00587.x

Lambeck, R. J. (1997). Focal species: a multi-species umbrella for nature conservation. *Conservation Biology*, *11*, 849–856.

Lane, S. J., & Alonso, J. C. (2001). Status and extinction probabilities of great bustard (*Otis tarda*) leks in Andalucia, southern Spain. *Biodiversity and Conservation*, **10**, 893–910.

Lane, S. J., Alonso, J. C., & Martín, C. A. (2001). Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? *Journal of Applied Ecology*, **38**, 193–203.

Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. M., … Watt, A. D. (1998). Biodiversity inventories, indicators taxa and effects of habitat modification in tropical forest. *Nature*, **39**, 72–76. doi:10.1603/0046-225X-32.3.542

Leverington, F., Costa, K. L., Pavese, H., Lisle, A., & Hockings, M. (2010). A global analysis of protected area management effectiveness. *Environmental Management*, **46**, 685–698. doi:10.1007/s00267-010-9564-5

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, *15*, 237–240.

Lomba, A., Alves, P., Jongman, R. H. G., & Mccracken, D. I. (2015). Reconciling nature conservation and traditional farming practices: A spatially explicit framework to assess the extent of High Nature Value farmlands in the European countryside. *Ecology and Evolution*, **5**, 1031–1044. doi:10.1002/ece3.1415

Lopez-Jamar, J., Casas, F., Diaz, M., & Morales, M. B. (2010). Local differences in habitat selection by Great Bustards *Otis tarda* in changing agricultural landscapes: Implications for farmland bird conservation. *Bird Conservation International*, **21**, 328–341. doi:10.1017/s0959270910000535

Maczulak, A. (2010). *Biodiversity: Conserving Endangered Species*. New York: Facts on File Inc.

Magaña, M., Alonso, J. C., Alonso, J. A., Martín, C. A., Martín, B., & Palacín, C. (2011). Great bustard (*Otis tarda*) nest locations in relation to leks. *Journal of Ornithology*, **152**, 541–548.

Magaña, M., Alonso, J. C., Martín, C. A., Bautista, L. M., & Martín, B. (2010). Nest-site selection by great bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis*, **152**, 77–89.

Mantyka-pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, **18**, 1239–1252. doi:10.1111/j.1365-2486.2011.02593.x

Martín, C. A., Martínez, C., Bautista, L. M., & Martín, B. (2012). Population increase of the great bustard *Otis tarda* in its main distribution area in relation to changes in farming practices. *Ardeola*, **59**, 31–42.

Martín, C. A., Alonso, J. C., Alonso, J. A., Palacín, C., Magaña, M., & Martín, B. (2007). Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard *Otis tarda*. *Journal of Avian Biology*, **38**, 335–346. doi:10.1111/j.2007.0908-8857.03811.x

Martínez, C. (2008). Distribution, density and productivity of great bustards *Otis tarda* in northwestern Spain: a regional approach. *Journal of Ornithology*, *149*(4), 507–514.McCallum, M. L. (2015). Vertebrate biodiversity losses point to a sixth mass extinction. *Biodiversity and Conservation*, **24**, 2497–2519. doi:10.1007/s10531-015-0940-6

Matthews, A. (2013). Greening agricultural payments in the EU's Common Agricultural Policy. *Bio-Based and Applied Economics*, *2*, 1–27.

Messer, J. J., Linthurst, R. A., & Overton, W. S. (1991). An EPA program for monitoring ecological status and trends. *Environmental Monitoring and Assessment*, **17**, 67–78. doi:10.1007/BF00402462

Molinari-Jobin, A., Molinari, P., Breitenmoser-Würsten, C., Wölfl, M., Stanisa, C., Fasel, M., … Breitenmoser, U. (2003). *The pan-Alpine conservation strategy for the Lynx*. Report prepared for Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). Retrieved from http://www.carnivoreconservation.org/files/actionplans/coe/SN130-E.pdf

Mollot, G., Pantel, J. H., & Romanuk, T. N. (2017). The Effects of Invasive Species on the Decline in Species Richness: A Global Meta-Analysis. In D. A. Bohan, A. J. Dumbrell, & F. Massol (Eds.), *Advances in Ecological Research* (1st ed., Vol. 56, pp. 61–83). Elsevier Ltd. doi:10.1016/bs.aecr.2016.10.002

Martínez, C. (2008). Distribution, density and productivity of great bustards *Otis tarda* in northwestern Spain: a regional approach. *Journal of Ornithology*, **149**, 507–514.

Mora, C., & Sale, P. F. (2011). Ongoing global biodiversity loss and the need to move beyond protected areas: A review of the technical and practical shortcomings of protected areas on land and sea. *Marine Ecology Progress Series*, **434**, 251–266. doi:10.3354/meps09214

Morales, M. B., Alonso, J. C., & Alonso, J. (2002). Annual productivity and individual female reproductive success in a Great Bustard *Otis tarda* population. *Ibis*, **144**, 293–300.

Morales, M. B., Jiguet, F., & Arroyo, B. (2001). Exploded leks: What bustards can teach us. *Ardeola*, **48**, 85–98.

Moreira, F., Leitão, P. J., Synes, N. W., Alcazar, R., Catry, I., Carrapato, C., … Osborne, P. E. (2012). Population trends in the steppe birds of Castro Verde in the period 2006-2011: consequences of a drought evens and land use changes? *Airo*, **22**, 79–89.

Morgado, R., & Moreira, F. (2000). Seasonal population dynamics, nest site selection, sex-ratio and clutch size of the great bustard *Otis tarda* in two adjacent lekking areas. *Ardeola*, **47**, 237-246.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, **520**, 45–50. doi:10.1038/nature14324

Ngo, T. D., & Webb, E. L. (2017). Reconciling Science and Indigenous Knowledge in Selecting Indicator Species for Forest Monitoring. In *Redefining Diversity & Dynamics of Natural Resources Management in Asia, Volume 3* (pp. 125–138). Elsevier. doi:10.1016/B978-0-12-805452-9.00009-6

Nichols, J. D., & Williams, B. K. (2006). Monitoring for conservation. *Trends in Ecology and Evolution*, **21**, 668–673. doi:10.1016/j.tree.2006.08.007

North American Bird Conservation Initiative (2007). *Opportunities for Improving Avian Monitoring*. U.S. North American Bird Conservation Initiative (NABCI) Monitoring Subcommittee, Arlington, VA. Retrieved from http://www.nabci-us.org/

North American Bird Conservation Initiative (2017). *State of North America's Birds 2016*. Retrieved from http://www.stateofthebirds.org/2016/

Oparin, M. L., Kondratenkov, I. A., & Oparina, O. S. (2003). Abundance of the Transvolga population of great bustard (*Otis tarda* L.). *Biology Bulletin*, **30**, 562–569.

Oparin, M. L., Oparina, O. S., Kondratenkov, I. A., Mamaev, A. B., & Piskunov, V. V. (2013). Factors causing long-term dynamics in the abundance of the Trans-Volga great bustard (*Otis tarda* L.) population. *Biology Bulletin*, **40**, 843–853. doi:10.1134/S1062359013100063

Osborne, P. E., & Seddon P. J. (2012). Selecting suitable habitats for reintroductions: variation, change and the role of species distribution modelling. In J. G. Ewen, D. P. Armstrong, K. A. Parker, & P. J. Seddon (Eds.), *Reintroduction biology: Integrating science and management*. Blackwell Publishing Ltd.

Osborne, P. E., Alonso, J. C., & Bryant, R. G. (2001). Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology*, *38*(2), 458–471.

Otis, D. L. (2006). Mourning dove hunting regulation strategy based on annual harvest statistics and banding data. *Journal of Wildlife Management*, **70**, 1302–1307. doi:10.2193/0022-541X(2006)70[1302:MDHRSB]2.0.CO;2

PAD-US Partnership (2009). *A Map for the Future: Creating the Next generation of protected Area Inventories in the United States*. The Protected Areas Database–U.S. (PAD-US) Partnership. Retrieved from www.protectedlands.net

Pakkala, T., Lindén, A., Tiainen, J., Tomppo, E., & Kouki, J. (2014). Indicators of forest biodiversity: Which bird species predict high breeding bird assemblage diversity in boreal forests at multiple spatial scales? *Annales Zoologici Fennici*, **51**, 457–476. doi:10.5735/086.051.0501

Palacín, C., & Alonso, J. C. (2018). Failure of EU biodiversity strategy in Mediterranean farmland protected areas. *Journal for Nature Conservation*, **42**, 62–66. doi:10.1016/j.jnc.2018.02.008

Palacín, C., Alonso, J. C., Alonso, J. A., Magaña, M., & Martín, C. A. (2011). Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard *Otis tarda*. *Journal of Avian Biology*, **42**, 301–308. doi:10.1111/j.1600-048X.2011.05395.x

Palacín, C., Alonso, J. C., Alonso, J. A., Martín, C. A., Magaña, M., & Martin, B. (2009). Differential migration by sex in the great bustard: possible consequences of an extreme sexual size dimorphism. *Ethology*, **115**, 617–626. doi:10.1111/j.1439-0310.2009.01647.x

Palacín, C., Alonso, J. C., Martín, C. A., & Alonso, J. A. (2016). Changes in bird-migration patterns associated with human-induced mortality. *Conservation Biology*, **31**, 106–115. doi:10.1111/cobi.12758

Parrish, J. D., Braun, D. P., & Unnasch, R. S. (2003). Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience*, **53**, 823–832. doi:10.1641/0006-3568(2003)053

Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., … Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, **344**, 1090–1092. doi:10.1126/science.1253425

Perkins, A. J., Maggs, H. E., Watson, A., & Wilson, J. D. (2011). Adaptive management and targeting of agri-environment schemes does benefit biodiversity: A case study of the corn bunting Emberiza calandra. *Journal of Applied Ecology*, **48**, 514–522. doi:10.1111/j.1365-2664.2011.01958.x

Pimm, S., Raven, P., Peterson, A., Sekercioglu, C. H., & Ehrlich, P. R. (2006). Human impacts on the rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of Sciences*, ***103***, 10941–10946. doi:10.1073/pnas.0604181103

Pinto, M., Rocha, P., & Moreira, F. (2005). Long-term trends in great bustard (*Otis tarda*) populations in Portugal suggest concentration in single high quality area. *Biological Conservation*, **124**, 415–423. doi:10.1016/j.biocon.2005.01.047

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology and Evolution*, **22**, 583–592. doi:10.1016/j.tree.2007.10.001

Proença, V., Martin, L. J., Pereira, H. M., Fernandez, M., McRae, L., Belnap, J., … van Swaay, C. A. M. (2017). Global biodiversity monitoring: From data sources to Essential Biodiversity Variables. *Biological Conservation*, **213**, 256–263. doi:10.1016/j.biocon.2016.07.014

Queiroz, C., Beilin, R., Folke, C., & Lindborg, R. (2014). Farmland abandonment: Threat or opportunity for biodiversity conservation? A global review. *Frontiers in Ecology and the Environment*, **12**, 288–296. doi:10.1890/120348

Raab, R., Julius, E., Greis, L., Schütz, C., Spakovszky, P., Steindl, J., & Schönemann, N. (2014). Endangering factors and their effect on adult Great Bustards (*Otis tarda*) — conservation efforts in the Austrian LIFE and LIFE+ projects. *Aquila*, **121**, 49–63.

Raab, R., Kollar, H. P., Winkler, H., Faragó, S., Spakovszky, P., Chavko, J., … Schütz, C. (2010). Development of the West Pannonian population of the Great Bustard, *Otis tarda*

Linnaeus 1758, from 1900 to the winter 2008/2009. *Egretta*, **51**, 74–99.

Ram, D., Axelsson, A. L., Green, M., Smith, H. G., & Lindström, Å. (2017). What drives current population trends in forest birds – forest quantity, quality or climate? A large-scale analysis from northern Europe. *Forest Ecology and Management*, **385**, 177–188. doi:10.1016/j.foreco.2016.11.013

Reidsma, P., Tekelenburg, T., Van Den Berg, M., & Alkemade, R. (2006). Impacts of land-use change on biodiversity: An assessment of agricultural biodiversity in the European Union. *Agriculture, Ecosystems and Environment*, **114**, 86–102. doi:10.1016/j.agee.2005.11.026

Ricotta, C., Carboni, M., & Acosta, A. T. R. (2015). Let the concept of indicator species be functional! *Journal of Vegetation Science*, **26**, 839–847. doi:10.1111/jvs.12291

Rocha, P., Marques, A. T., & Moreira, F. (2005). Seasonal variation in Great Bustard *Otis tarda* diet in south Portugal with a focus on the animal component. *Ardeola*, **52**, 371–376.

Rocha, P., Morales, M. B., & Moreira, F. (2012). Nest site habitat selection and nesting performance of the great bustard *Otis tarda* in southern Portugal: Implications for conservation. *Bird Conservation International*, **23**, 323–336. doi:10.1017/s0959270912000202

Sala, O. E., & Paruelo, J. M. (1997). Ecosystem services in grasslands. In G. Daily (Ed.), *Nature's Services: Societal Dependence on Natural Ecosystems*. Washington DC: Island Press.

Sánchez, A., & Garcia - Baquero, M. J. (2012). La avutarda en Badajoz: estabilidad, pero con matices. *Quercus*, *314*, 16–22.

Santana, J., Reino, L., Stoate, C., Borralho, R., Carvalho, C. R., Schindler, S., … Beja, P. (2014). Mixed effects of long-term conservation investment in Natura 2000 farmland. *Conservation Letters*, **7**, 467–477. doi:10.1111/conl.12077

Santana, J., Reino, L., Stoate, C., Moreira, F., Ribeiro, P. F., Santos, J. L., … Beja, P. (2017). Combined effects of landscape composition and heterogeneity on farmland avian diversity. *Ecology and Evolution*, **7**, 1212–1223. doi:10.1002/ece3.2693

Schwandner, J., & Langgemach, T. (2011). How much habitat is left for the great bustard (*Otis tarda*)? Human infrastructure and remaining suitable habitat in western

Brandenburg (Germany). *Berichte Zum Vogelschutz*, **47**, 193–206.

Shea, K., Roxburgh, S. H., & Rauschert, S. J. (2004). Moving from pattern to process: Coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters*, **7**, 491–508. doi:10.1111/j.1461-0248.2004.00600.x/abstract

Silva, J. P., Correia, R., Alonso, H., Martins, R. C., D'Amico, M., Delgado, A., … Moreira, F. (2018). EU protected area network did not prevent a country wide population decline in a threatened grassland bird. *PeerJ*, **6**, e4284. doi:10.7717/peerj.4284

Silva, J. P., Toland, J., Jones, W., Elridge, J., Thorpe, E., & O'Hara, E. (2008). *LIFE and Europe's grasslands: Restoring a forgotten habitat*. (P. Owen, Ed.). Luxembourg. doi:/10.2779/23028

Simberloff, D. (1998). Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? *Biological Conservation*, **83**, 247–257.

Soulé, M. E. (1985). What is conservation biology? A new synthetic discipline addresses the dynamics and problems of perturbed species, communities, and ecosystems. *BioScience*, **35**, 727–734.

Steffen, W., Sanderson, A., Tyson, P. D., Jäger, J., Matson, P. A., Moore, B. I., … Wasson, R. J. (2004). *Global Change and the Earth System: A Planet under Pressure*. Berlin: Springer.

Stem, C., Margoluis, R., Salafsky, N., & Brown, M. (2005). Monitoring and evaluation in conservation: A review of trends and approaches. *Conservation Biology*, **19**, 295–309.

Streich, W. J., Litzbarski, H., Ludwig, B., & Ludwig, S. (2006). What triggers facultative winter migration of Great Bustard (*Otis tarda*) in Central Europe? *European Journal of Wildlife Research*, **52**, 48–53.

Suárez, F., Naveso, M. A., & De Juana, E. (1997). Farming in the drylands of Spain: birds of the pseudosteppes. In D. J. Pain & M. W. Pienkowski (Eds.), *Farming and Birds in Europe. The Common Agricultural Policy and its Implications for Bird Conservation.* (pp. 297–330). San Diego: Academic Press.

Sullivan, B. L., Aycrigg, J. L., Barry, J. H., Bonney, R. E., Bruns, N., Cooper, C. B., … Kelling, S. (2014). The eBird enterprise: An integrated approach to development and application of citizen science. *Biological Conservation*, **169**, 31–40. doi:10.1016/j.biocon.2013.11.003

Sullivan, B. L., Phillips, T., Dayer, A. A., Wood, C. L., Farnsworth, A., Iliff, M. J., … Kelling, S. (2017). Using open access observational data for conservation action: A case study for birds. *Biological Conservation*, **208**, 5–14. doi:10.1016/j.biocon.2016.04.031

Sunderlin, W. D., Belcher, B., Santoso, L., Angelsen, A., Burgers, P., Nasi, R., & Wunder, S. (2005). Livelihoods, forests, and conservation in developing countries: An overview. *World Development*, **33,** 1383–1402. doi:10.1016/j.worlddev.2004.10.004

Sutcliffe, L. M. E., Batáry, P., Kormann, U., Báldi, A., Dicks, L. V., Herzon, I., … Tscharntke, T. (2015). Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity and Distributions*, **21**, 722–730. doi:10.1111/ddi.12288

Tarjuelo, R., Morales, M., Arroyo, B., Mañosa, S., Bota, G., Casas, F., & Traba, J. (2017). Intraspecific and interspecific competition induces dependent habitat niche shifts in an endangered steppe bird. *Ecology and Evolution*, **7**, 1–11. doi:10.1002/ece3.3444

Tarjuelo, R., Morales, M. B., Traba, J., & Delgado, M. P. (2014). Are species coexistence areas a good option for conservation management? Applications from fine scale modelling in two steppe birds. *Plos One*, **9**, 1–9. doi:10.1371/journal.pone.0087847.g001

Tarjuelo, R., Traba, J., Morales, M. B., & Morris, D. W. (2016). Isodars unveil asymmetric effects on habitat use caused by competition between two endangered species. *Oikos*, **125**. doi:10.1111/oik.03366

Tautin, J., Metras, L., & Smith, G. (1999). Large-scale studies of marked birds in North America. *Bird Study*, **46**, S271–S278. doi:10.1080/00063659909477254

Thébault, A., Mariotte, P., Lortie, C. J., & Macdougall, A. S. (2014). Land management trumps the effects of climate change and elevated CO_2 on grassland functioning. *Journal of Ecology*, **102**, 896–904. doi:10.1111/1365-2745.12236

Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, **108**, 20260–20264. doi:10.1073/pnas.1116437108

Timko, J. A., & Innes, J. L. (2009). Evaluating ecological integrity in national parks: Case studies from Canada and South Africa. *Biological Conservation*, **142**, 676–688. doi:10.1016/j.biocon.2008.11.022

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., … Whitbread,

A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, **151**, 53–59. doi:10.1016/j.biocon.2012.01.068

UNEP-WCMC (2018). *Protected Area Profile for United States of America from the World Database of Protected Areas, March 2018*. Retrieved from www.protectedplanet.net

Vadász, C., & Lóránt, M. (2014). Key mortality causes of the Great Bustard (*Otis tarda*) in Central Hungary: an analysis of known fatalities. *Ornis Hungarica*, **22**, 32–41. doi:10.2478/orhu-2014-0016

Van Dyke, F. (2008). *Conservation Biology: Foundations, Concepts, Applications* (Second). Berlin: Springer.

van Strien, A., Pannekoek, J., Hagemeijer, W., & Verstrael, T. (2004). A loglinear poisson regression method to analyse bird monitoring data. *Bird Census News*, **13**, 33–39.

van Swaay, C. A. M., van Strien, A. J., Aghababyan, K., Åström, S., Botham, M., Brereton, T., … Warren, M. S. (2015). *The European Butterfly Indicator for Grassland species: 1990-2013*. Butterfly Conservation Europe, Wageningen, NL.

van Vliet, J., de Groot, H. L. F., Rietveld, P., & Verburg, P. H. (2015). Manifestations and underlying drivers of agricultural land use change in Europe. *Landscape and Urban Planning,* **133**, 24-36. doi:10.1016/j.landurbplan.2014.09.001

Vandewalle, M., de Bello, F., Berg, M. P., Bolger, T., Dolédec, S., Dubs, F., … Woodcock, B. A. (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, **19**, 2921–2947. doi:10.1007/s10531-010-9798-9

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., … Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, **7**, 1–11. doi:10.1038/ncomms12558

Veríssimo, D., Fraser, I., Girão, W., Campos, A. A., Smith, R. J., & Macmillan, D. C. (2014). Evaluating conservation flagships and flagship fleets. *Conservation Letters*, **7**, 263–270. doi:10.1111/conl.12070

Wade, A. S. I., Barov, B., Burfield, I. J., Gregory, R. D., Norris, K., Vorisek, P., … Butler, S. J. (2014). A niche-based framework to assess current monitoring of European forest birds and guide indicator species' selection. *PLoS ONE*, **9**, e97217.

doi:10.1371/journal.pone.0097217

Wright, H. L., Lake, I. R., & Dolman, P. M. (2012). Agriculture-a key element for conservation in the developing world. *Conservation Letters*, **5**, 11–19. doi:10.1111/j.1755-263X.2011.00208.x

Chapter 2

Mixed trends of Great Bustard *Otis tarda* subpopulations in Extremadura (Spain) and Alentejo (Portugal)

Yoav Perlman[1*], João P. Silva[2, 3], Marcia V. Pinto[4], Pedro Rocha[4], Angel Sánchez[5], Joachim Hellmich[6], Alastair Grant[1], Robert J. Bunside[1], Nigel J. Collar[7, 8], and Paul M. Dolman[1]

[1] School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom; [2] Centro de Ecologia Aplicada 'Prof. Baeta Neves', Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal; [3] Centro de Ecologia, Evolucão e Alteracões Climáticas, Faculdade de Ciéncias, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portuga; [4] Departmento de Conservação da Natureza e Florestas do Alentejo, Instituto da Conservação da Natureza e das Florestas, IP, Rua Tenente Raul D'Andrade, 1 e 3 7000-613, Evora, Portugal; [5] Servicio de Conservacíon de la Naturaleza, y Areas Protegidas, Consejaria de Agricultura, Desarrollo Rural, Medio Ambiente y Energía, Gobierno de Extremadura, Avda. Luis Romallo s/n, 06800-Merida, Spain; [6] World Wildlife Fund, Gran Via de San Francisco, 28005 Madrid, Spain; [7] BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, United Kingdom; [8] School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom.

Submitted paper Oryx (submitted 03/11/2017, referee comments received 11/12/2017)

2.1 Abstract

Up to 27% of the Iberian population of the globally Vulnerable Great Bustard *Otis tarda* occurs in Extremadura (Spain) and adjacent Alentejo (Portugal). Estimates of breeding numbers in these areas have been uncoordinated and used divergent methods. We explored the appropriate spatial scales at which to identify subpopulation trends, examined whether subpopulation trends varied spatially and temporally, tested whether subpopulation trends were linked with SPA declaration, and updated population estimates for the study area. Using spring counts between 1980 and 2014, we recognise 16 'subpopulations' as distinct demographic units. Subpopulation-specific trends varied during the study period: numbers in four subpopulations decreased significantly, and increased significantly in three subpopulations. We used generalised linear models examining subpopulation temporal trends to estimate that overall breeding numbers, derived from models, decreased from 3,614 in 1985 (95% CI 3,484–3,747) to 2,548 (2,414–2,678) in 2002, but increased to 4,610 (4,474–4,712) in 2014, with model estimates for 1985 and 2011 consistent with actual counts. Between 2010 and 2014 actual counts apparently declined by 30% from 4,966 to 3,512, and continued in parts of the region until 2017, although the selected quadratic structure of the generalised linear models was unable to represent more recent declines. The latest actual count is much lower than previously published figures. No trend differences were found between Extremadura and Alentejo, and there is no evidence that SPA declaration has meaningfully altered trends across these subpopulations. The potential causes of these trends, especially concerning agricultural land-use change, require urgent study.

2.2 Introduction

The Great Bustard *Otis tarda* is Europe's heaviest flying bird, with extreme sexual dimorphism related to its lekking mating system (Alonso *et al.* 2009, Collar & Garcia 2018). In this unique breeding system, males concentrate in display arenas, to which females are attracted to copulate (Alonso, Álvarez-Martínez & Palacín 2012; Morales, Jiguet & Arroyo 2001). Because of sexual differences in mortality rates (Martín *et al*. 2007; Palacín *et al.* 2016), in most populations sex-ratios are skewed towards females (see Section 1.5).

Despite research and conservation over many decades (see Alonso 2014), the Great Bustard remains a threatened species (IUCN Vulnerable: BirdLife International 2018). Global numbers were judged to have declined by over 30% from the 1960s to 1982 (Collar 1985), but then increased from an estimated 27,000 in 1991 (Collar 1991) to between 44,100 and 57,000 individuals in 2010 (Palacín and Alonso 2008, Alonso and Palacín 2010). This increase has been explained by two processes: (1) real numerical augmentation in Iberia, from 17,000–19,000 in the 1990s to 24,000–34,300 in 2010 (Alonso and Palacín 2010) and (2) improved information on the species' range permitting more accurate counts and population estimates (Alonso & Palacín 2010). Nevertheless, the main threats to Great Bustard conservation remain loss, fragmentation and degradation of habitat through land-use change, and decreased survival through infrastructure development (Nagy 2009). More specifically, intensification of low-intensity agricultural systems are thought to have caused population declines in several central and eastern European countries (Faragó, Spakovszky & Raab 2014; Oparin *et al*. 2013; Raab *et al*. 2010; Schwandner & Langgemach 2011). Additionally, powerline collision mortality is a

major threat to Great Bustards worldwide (Alonso 2014). Conservation institutions seeking to manage the species effectively against these threats therefore need regular updates on population sizes and trends, especially in Iberia where 57–70% of the global population is judged to occur (Alonso & Palacín 2010).

The population and conservation status of the Great Bustard in south-west Iberia (Fig. 2.1), i.e. Extremadura (Spain; with two provinces, Cáceres and Badajoz) and Alentejo (in adjacent Portugal), is not well understood. Estimates for Extremadura indicated 5,500–6,500 individuals in 2005, with 3,500–4,000 in Badajoz and 2,000–2,500 in Cáceres (Corbacho *et al.* 2005). More recently 1,653 birds were estimated in Badajoz for 2011 (Sánchez & Garcia-Baquero 2012), suggesting a major decline. In the Alentejo, which holds the entire Portuguese breeding population, numbers were 1,150 in 2002 (Pinto *et al.* 2005) but 1,893 in 2009 (in Alonso & Palacín 2010), suggesting a major increase. Together these published counts for Extremadura (updated for 2005, based on data from 2002–2003: Corbacho *et al.* 2005) and Alentejo (updated for 2009: Alonso & Palacín 2010) comprise 20–27% of the estimated total Iberian population of 31,293–36,193 (Alonso & Palacín 2010). These published counts for Extremadura and Alentejo are outdated, and require update. Additionally, because of the relatively large number of Great Bustards in Extremadura and Alentejo, and indications of mixed trends in parts of the region (Pinto *et al.* 2005), there is a need for a clear picture of local and overall trends in this important region.

To improve the conservation status of agro-steppe bird species in the region, including the Great Bustard, 21 Special Protection Areas (SPAs) (eight in

Extremadura, 13 in Alentejo) have been designated under the EC Birds Directive (Directive 79/409/EEC) under Natura 2000 network (European Commission 2017, see Table 2.1). However, large-scale effective conservation measures, starting in 1993 and including the restriction of irrigation, afforestation and perennial crops plus the adjustment of harvest cycles, have been documented only for a single SPA in the region, Castro Verde in southern Alentejo (Pinto *et al.* 2005; Santana *et al.* 2014). These measures were judged to have increased Great Bustard local productivity and attracted immigrants from other areas (Pinto *et al.* 2005); the abundance of the species was certainly higher inside than outside this SPA (Santana *et al.* 2014). Some conservation interventions, such as fence and powerline markings to reduce collisions, and restriction of open habitat conversion (YP, JPS pers. obs.), have been implemented in the other 20 SPAs, but documentation and evidence of their effectiveness are both lacking. Other than in Castro Verde the conservation status of Great Bustards in the Alentejo is alarming, with extirpations in eight (44%) of 18 known sites in the short period 1980–2002 (Pinto *et al.* 2005). No recent information on status and trends of Great Bustards in Extremadura and Alentejo has been published.

Until now the Great Bustard populations of Extremadura and Alentejo have been studied and managed independently, even though some areas for the species are adjacent and even contiguous across the international frontier (Pinto *et al.* 2005). Moreover, the methods for identifying and monitoring populations in the two regions have been somewhat different. Population assessments in the region have focused on lekking areas—display concentrations of males in spring (Alonso *et al.* 2012). Lekking areas are the focal points used in Alentejo to identify

conservation units (Pinto *et al.* 2005). In Extremadura, conservation units labelled "sub-nuclei", lie within wider zones ("nuclei"), judged by accumulated experience to encompass the areas occupied by breeding females (Corbacho *et al.* 2005). Conservation units in Alentejo except Castro Verde therefore exclude potential breeding areas between leks (Magaña *et al.* 2011, Alonso *et al.* 2000) and treat adjacent localities (e.g. 5 km apart) as distinct, even though they may frequently exchange individuals (PR, MVP, JPS, YP unpubl. data).

This study describes overall changes in Great Bustard numbers across the unified region of Extremadura and Alentejo between 1985 and 2015, seeking to update and standardise population estimates for this important region. This study identifies the spatial scale at which Great Bustard groups into meaningful demographic units used to track local changes in numbers, based on classic metapopulation theory concepts (Levins 1969). Additionally, this study sought to describe regional patterns that may explain changes in local population numbers, notably differences in local trends Extremadura and Alentejo, and whether declaration of SPAs altered local trends within them.

Table 2.1: Pseudo-steppe SPAs in Extremadura and Alentejo. Subpopulation names that overlap with SPAs correspond with Figure 2.2a.

Province	***SPA name***	***Overlaps with subpopulation***	***Year designated***	***Area (ha)***	***% overlap with subpopulation***
Badajoz	*Campiña Sur - Embalse de Arroyo Conejos*	*Campiña Sur*	*2004*	*44809*	*100*
Badajoz	*La Serena y Sierras Periféricas*	*La Serena*	*2000*	*154974*	*72*
Badajoz	*Llanos y Complejo Lagunar de la Albuera*	*NAWB*	*2004*	*36463*	*71*
Cáceres	*Llanos de Alcantara y Brozas*	*Central Cáceres*	*2004*	*46579*	*97*
Cáceres	*Llanos de Cáceres y Sierra de Fuentes*	*Central Cáceres*	*1989*	*69665*	*100*
Cáceres	*Llanos de Trujillo*	*Central Cáceres*	*2003*	*7707*	*100*
Cáceres	*Magasca*	*Central Cáceres*	*2004*	*10869*	*100*
Cáceres	*Llanos de Zorita y Embalse de Sierra Brava*	*Campo Lugar*	*2003*	*18696*	*100*
Alentejo	*Campo Maior*	*NAWB*	*1999*	*9579*	*73*
Alentejo	*Mourão / Moura / Barrancos*	*Villanueva del Fresno and Mourão*	*1999*	*80608*	*51*
Alentejo	*Castro Verde*	*Castro Verde*	*1999*	*79007*	*100*
Alentejo	*Vale do Guadiana*	*Castro Verde*	*1999*	*76547*	*54*
Alentejo	*Monforte*	*NAWB*	*2008*	*1887*	*100*
Alentejo	*Veiros*	*NAWB*	*2008*	*1959*	*100*
Alentejo	*Vila Fernando*	*NAWB*	*2008*	*5260*	*100*
Alentejo	*São Vicente*	*NAWB*	*2008*	*3565*	*35*
Alentejo	*Évora*	*Evora*	*2008*	*14707*	*100*
Alentejo	*Reguengos*	*Villanueva del Fresno and Mourão*	*2008*	*6043*	*3*
Alentejo	*Cuba*	*Cuba*	*2008*	*4081*	*100*
Alentejo	*Piçarras*	*Castro Verde*	*2008*	*2827*	*100*
Alentejo	*Torre de Bolsa*	*NAWB*	*2008*	*869*	*100*

2.3 Methods

2.3.1 Data sources, reliability and comparability

Great Bustard numbers have been monitored in both Extremadura and the Alentejo (Fig. 2.1) since the early 1980s. In Extremadura the Junta de Extremadura (regional government) has counted Great Bustards in spring since 1981, but not annually or consistently between provinces (13 and 10 counts in Cáceres and Badajoz respectively between 1981 and 2015) (Corbacho *et al.* 2005; Sánchez and Garcia-Baquero 2012, AS unpublished data). Independently, JH conducted five counts across Cáceres province at four-year intervals between 1999 and 2015, in years not surveyed by the Junta de Extremadura. In the Alentejo, annual spring counts were conducted from 1980 to 2014, with a four-year gap between 1996 and 1999 (Pinto *et al.* 2005). For 2013 and 2014, counts for some peripheral areas of the Castro Verde (southern Alentejo) subpopulation were not available; however, counts from the surveyed part for these years were included in the analyses as the missing sections had previously contributed only 5.4% (years 2002–2012, mean 59 Great Bustards, range 39–131, SD = 38) of the mean count for the greater Castro Verde (mean=1,100). A list of data used in analyses and a table of count results are available in Appendices 2.1 and 2.2.

Figure 2.1: Study area in relation to south-western Europe. Borders of Extremadura (Spain) and Alentejo (Portugal) in thick black lines; border between provinces of Cáceres and Badajoz in dashed line.

Since their inception, counts in the region have conformed with principles subsequently formalised by Alonso *et al.* (2005) relating to timing, experience of personnel and accessibility of areas. Counts are here judged most efficient in the spring display season (March–April), owing to a combination of factors: males concentrate in leks to display and are thus very visible, females also concentrate to copulate, heat-haze is relatively weak during morning census work, and vegetation cover is both shorter (allowing more visibility) and greener (providing greater contrast with the birds' plumage) (Alonso *et al.* 2005a, 2012, NJC pers. obs.). Counts were conducted by the same personnel from one survey to the next throughout the

entire study period, professional ornithologists and rangers, all familiar with the species, the survey areas and the local landowners, and all using 4×4 vehicles to access all areas.

In Extremadura, locations of birds were recorded on maps and later digitised to create spatially explicit layers. In Alentejo, counts were available per site, and not as spatially explicit layers. Across Extremadura and Alentejo, only a small proportion (mean 4.5%, SD = 12.5%) could not also be recorded by sex or age, but Junta de Extremadura counts (n = 34, mean = 10.0%, SD = 1.56%) had a higher percentage of unclassified birds than other data sources (n = 108, mean = 3.1%, SD = 1.09%, $F_{1, 141} = 8.023$, $p<0.01$). Unclassified birds were excluded from adult male figures but included in total numbers.

One potential source of error concerns the misidentification of females as yearling males, or vice versa. Their difference in plumage is slight, while the considerable size difference is not easy to gauge at a distance and with no adult males for reference (Alonso *et al.* 2005). The ratio of yearling males to females was lower in Junta de Extremadura counts (mean = 0.05, SE = 0.011) than for other data sources (mean = 0.21, SE = 0.026, $F_{1, 205} = 25.3$, $p<0.001$). This difference might relate to true regional differences in productivity and recruitment resulting from local management interventions differentially affecting breeding success. It might, however, result (at least in part) from methodological differences: in count timing (so that fewer females are present if counts occur after the peak lekking season) and/or in field skills, potentially resulting in different detection rates and the mis-classification of the individuals detected. As we cannot be confident that

differences in relative numbers of yearling males to females represent biological differences rather than sampling error we have not attempted separate analyses of females and yearling males. Nevertheless, both total counts, and counts of adult males, are not affected by such classification error.

Censuses by the Junta de Extremadura involved multiple teams working simultaneously over 1–2 days across the entire area, to minimise a perceived risk of double-counting. However, census dates were fixed long in advance and could not be adjusted to weather conditions or variations in timing of breeding season (AS), so counts were more likely to underestimate numbers of females (which concentrate for shorter periods than the males) than other age or sex classes. In the period 1980–1995 surveys in the Alentejo were conducted by a single team making multiple site visits within the display season, with the highest count registered as the most accurate record; but since 2000 these surveys have generally followed the method of the Junta de Extremadura.

For our analyses we used long time series, and analysed total counts, given that these are methodologically consistent across time, sites and teams even if subject to greater sampling error due to underestimates of the more cryptic females in sites or years when count timing did not coincide with the peak of lek attendance. Separately, we examined temporal trends in counts of adult males (for which sampling errors and differences among survey teams were expected to be minimal).

2.3.2 Definition of subpopulations as demographic units

To minimise the risk that inter-annual variation in counts merely reflects localised movements and chance sampling, we defined demographic units based on empirical evidence that shows that adult males and females are faithful to breeding areas over a scale of several kilometres. A small proportion of females (1 of 55 tagged individuals, 2%) in central Spain attended different lekking sites c. 5 km apart within one season (Magaña *et al.* 2011) and 2 of 27 tagged females (7%) in north-western Spain attended different lekking sites 2–10 km apart in successive years (Alonso *et al.* 2000). A single tagged adult male out of a sample of 13 (8%) in north-western Spain visited multiple lekking sites about 10 km apart within a season and among years, while 12 showed high fidelity to the same lek (Morales *et al.* 2000). In finer resolution, adult males have been observed to move between lekking sites about 5 km apart (YP, JPS pers. obs.). Furthermore, 64% of tagged females in central Spain nested outside of the lekking area they had attended, and often closer to other lekking sites (Magaña *et al.* 2011).

In this study, the biological definition of semi-independent subpopulations was based on classic metapopulation theory (Levins 1969), in which changes in numbers within subpopulations are a result of changes in demographic rates (productivity, recruitement, immigtaion, mortality), and not as a result of local movements that may cause underestimates or double counting. While some yearling and subadult males may immigrate between subpopulations, adult males and females are highly philopatric (Alonso *et al.* 1998, 2004; Martín *et al.* 2002, 2008; Rocha 2006) and the changes in counts in subpopulations are likely to represent actual changes in numbers in those subpopulations. We therefore

defined subpopulation units by buffering and aggregating lekking areas in the Alentejo and Extremadura to include the potential area where females breed. To determine the most appropriate buffer distance by which to delineate demographic units (hereafter 'subpopulations'), we compared the temporal variance explained by models aggregating spatially explicit count data from Extremadura into units defined by buffers at scales from 3 km to 15 km (see below).

2.3.3 Buffer scale for subpopulaton definition

To test at what scale aggregation of census data into subpopulation units improved the ability to explain temporal trends, we examined spatially-explicit data from Extremadura only (not Alentejo) available for years 1985, 1988, 1993, 1999 (partial, i.e. only small parts of Extremadura surveyed), 2002, 2003 (partial), 2004 (partial), 2005 (partial), 2010, 2011, 2012 and 2014. A grid of 3 km × 3 km was overlaid on each annual count layer in ArcMap (ESRI 2014), and annual totals per cell calculated (n= 393 cells with one or more counts; cells where bustards were not found in any year were excluded). Of the 2,612 annual cell totals used for the model, 940 (36%) had a count of one bird or more. A baseline generalised linear mixed model (GLMM) related annual count per grid cell to year (coded as 1999=0 to centralise data) and year^2 as fixed effects, with cell identity as a random factor to account for lack of independence of repeated counts. A second polynom of year was added to the model to represent potential natural processes in populations. A negative binomial error distribution (with log link) was the most appropriate (residual deviance / df= 0.84), as it avoided over-dispersion that can lead to biased parameter precision and poor inference (Richards 2008).

Using different aggregation buffers around male locations (3 km, 5 km, 7 km, 9 km, 12 km and 15 km), respectively 43, 22, 16, 12, 7 or 3 'subpopulations' were defined in Extremadura only. Buffers were created around male locations in 1985, 2002 and 2011, merging all intercepting buffers for each time snapshot (1985, 2002 or 2011), and then merging all intercepting buffers of the three different time snapshots to create a maximum extent across the entire study period. Further GLMMs of temporal changes of annual (all available years) counts per cell were developed, again including fixed effects of year, year^2, and cell ID as a random effect to account for repeated annual counts in the same cell, and fixed effect of the cell's unique 'subpopulation identifier', and the interaction between subpopulation and year (to account for different trends between subpopulations). To identify at which buffer size models have the strongest predictive power, these alternative models were compared using the Akaike Information Criterion (adjusted for small sample size; AICc). Subsequently, the best-supported buffer scale was applied to lekking sites (Alentejo) and spatially explicit observations (Extremadura) to define subpopulation units, with counts in each year summed within these subpopulations. Subsequent analyses considered observations per subpopulation per year.

2.3.4 Analysis of temporal trends

First counts of each subpopulation (from 1980 or 1981) were excluded from all analyses, as the initial inexperience of surveyors might have resulted in underestimates (Alonso *et al.* 2005). Counts of two cross-border subpopulations

(Northern Alentejo–Western Badajoz, and Mourão–Villanueva del Fresno) were included only in years when they took place on both sides of the border. Six sites holding fewer than six Great Bustards in two consecutive years between 1980 and 1985 (Pinto *et al.* 2005), and one location in Extremadura that held two males in 2002 only, were included in overall totals but excluded from subpopulation analyses. Trend analyses were conducted separately for total counts (n= 259 subpopulation-specific counts, excluding first counts and incomplete counts from cross-border subpopulations) and adult males (n=199).

For visualisation purposes, complex changes in numbers a second-order LOESS curve (a scatterplot-smoothing method based on fitting a locally weighted polynomial; Cleveland & Devlin 1988), was fitted with a smoothing parameter of 0.75 (so that each local prediction is based on 75% of the data). Because of difficulties of LOESS to deal with too many missing values, LOESS curves were not fitted for subpopulation time series comprising fewer than eight counts (excluding one subpopulation for total counts, and four for adult male counts). To examine changes in individual subpopulation size, subpopulation counts ($\log_{10}(1+n)$ transformed) were related to year using separate generalised linear models (GLMs) with normal error.

To examine temporal trends between 1985 and 2014 simultaneously across all subpopulations, annual subpopulation-specific counts ($\log_{10}(1+n)$ transformed) were related to year (with 1999 = 0) using GLMs with normal error, including subpopulation identifier as a fixed factor and the interaction between subpopulation and year. Potentially more complex patterns of population change

were then examined in a series of additional models that incorporated second- and third-order orthogonal polynomial terms of year (maintaining the independence of the linear slope; Bright & Dawkins 1965) and their interactions with subpopulation, to simulate natural processes in populations. The most parsimonious model was selected based on changes in AICc value. This temporal model was used to estimate the overall totals across Extremadura and Alentejo in each year (including years where one or more subpopulations lacked census data), by summing the subpopulation-specific estimates, with the 95% confidence interval (CI) of estimated totals obtained as the sum of the population-specific CI's.

The selected temporal model was then used to examine whether subpopulation trends differed between (A) Extremadura [reference level] and Alentejo [additive effect] (assigning subpopulations in Northern Alentejo–Western Badajoz and Mourão–Villanueva del Fresno to Extremadura and Alentejo, respectively, based on the greater area in each province), or (B) Castro Verde (and adjacent subpopulations Moreanes and Cuba) [reference level] and all remaining subpopulations [additive effect]; in each case incorporating both the relevant categorical variable and its interaction with year. To examine whether remaining Great Bustard numbers had concentrated within a few key sites, potentially continuing the process suggested by Pinto *et al*. (2005), a Gaussian GLM was performed relating the proportion (arcsine square-root transformed) of the Great Bustard count of the three subpopulations with the highest mean count between 1980 and 2014 (Castro Verde, Central Cáceres and Northern Alentejo–Western Badajoz; see Appendix 2.2) out of the total count for the entire region, to count

year, considering only those years with complete coverage (1985, 1988, 1993, 2002, 2010, 2011, 2012 and 2014).

In all cases, models were considered strongly supported if the AICc value reduced by at least 2 AICc units (Burnham & Anderson 2004) relative to alternative models.

Links between SPA designation and subpopulation trends

Information about SPA designation year and area was obtained from http://extremambiente.gobex.es/index.php?option=com_content&view=article&id=103&Itemid=461 (Extremadura) and http://www.icnf.pt/portal/pn/biodiversidade/rn2000/rn-pt/rn-contin/zpe-pt (Alentejo), summarized in Table 2.1, but data on the extent, duration and nature of conservation interventions in most of the 21 SPAs in the region are lacking. In addition to the TRIM analysis above, I sought to examine whether SPA declaration had long-term benefits for Great Bustard subpopulations. I used a GLM approach to test whether subpopulation trends were linked with SPA declaration. The recent linear trend in subpopulation count between 2010 and 2014 (calculated using $\log_{10}(1+n)$ counts) was related to the proportion of subpopulation area designated as SPA (arcsine-square-rooted) in a GLM with normal error.

TRIM analysis

Additionally, TRIM (Trends & Indices for Monitoring Data) analysis was carried out using 'rtrim' package in R (Bogaart *et al.* 2018) on the entire dataset of annual subpopulation total spring counts (not adult males). In this method, loglinear poisson regression methods allow estimations of annual indices and trends, and tests the effects of covariates (van Strien *et al.* 2004). This analysis was used to identify the overall linear trend for the entire study period, and to evaluate the importance of SPA declaration on trends. In the analysis, for each subpopulation count, SPA declaration was added as a covariate to the analysis. Using Wald test, the signifiance of the overall linear trend, and the effect of SPA declaration (whether SPA was declared at a specific subpopulation in a specific year, see Table 2.1) were tested.

All analyses were carried out in RStudio version 1.1.383 (R Core Team 2017), using packages lme4 (Bates *et al.* 2015) to carry out mixed modelling, rtrim (Bogaart *et al.* 2018) for TRIM analysis, and MuMIn (Bartoń 2013) to obtain AICc values.

2.4 Results

2.4.1 Identification of subpopulations

Initial GLMs showed that the attribution of individual counts per 3 km × 3 km grid cell to larger subpopulation units increased the explanatory power of models (Table 2.2). For every buffer scale, inclusion of an interaction term between subpopulation and year substantially reduced AICc relative to the model with only subpopulation identity, indicating that temporal trends differed among subpopulations. The best-supported models considered subpopulations buffered at scales of 3 km, 5 km, 7km and 9 km. Although models considering subpopulations based on 3 km and 5 km had the greatest reduction in AICc values compared to the null model (ΔAICc = -1233.09 and ΔAICc = -942.6 respectively, Table 2.2), adult males were observed moving between 'subpopulations' defined when leks were buffered at 3 km and 5 km (YP, JPS, MVP pers. obs.). Thus, these buffer sizes may fail to define subpopulations that contain all regular movements of adults within them. Models considering subpopulations based on 9 km buffers received much strong support (ΔAICc = -712.83) compared to models considering subpopulations based on 7 km buffers (ΔAICc = -539.22). Therefore, subpopulations based on 9 km buffers around male locations were selected as the most appropriate spatial scale for subsequent analysis of trends. Based on this, 16 subpopulations of Great Bustards were defined across the region (Figs. 2.2a and 2.2b).

Table 2.2: Results of generalised linear mixed models (with negative binomial error) for Great Bustards in Extremadura only between 1985 and 2014, relating changes in annual count totals per 3 km × 3 km cell (393 cells, 2,612 counts) to year, year^2, subpopulation identity (depending on scale of spatial aggregation) and the interaction of year and subpopulation identity. All models include cell identity as a random effect. ΔAICc values represent the change in AICc value compared to the baseline model (year and year^2, no aggregation of cells within subpopulations). ΔAICc values in **bold** represent strong support.

Model	***Subpopulation buffer radius***	***B***	***SE***	***AICc***	***ΔAICc***
Year *Year^2*		*0.004* *-0.003*	*0.001* *<0.001*	*36420.81*	*0*
Year *Year^2* *subpopulation*	*3 km (n=43)*	*0.003* *-0.003*	*0.001* *<0.001*	*36106.23*	***-314.58***
Year *Year^2* *Subpopulation* *Subpopulation*year*		*-0.004* *-0.001*	*0.004* *<0.001*	*35187.72*	***-1233.09***
Year *Year^2* *Subpopulation*	*5 km (n=22)*	*0.004* *-0.003*	*0.001* *<0.001*	*36145.72*	***-275.09***
Year *Year^2* *Subpopulation* *Subpopulation*year*		*-0.004* *-0.001*	*0.004* *<0.001*	*35478.21*	***-942.6***
Year *Year^2* *Subpopulation*	*7 km (n=16)*	*0.004* *-0.003*	*0.001* *<0.001*	*36411.82*	***-8.99***
Year *Year^2* *Subpopulation* *Subpopulation*year*		*0.177* *-0.004*	*0.044* *<0.001*	*35881.59*	***-539.22***
Year *Year^2* *Subpopulation*	*9 km (n=12)*	*0.004* *-0.003*	*0.001* *<0.001*	*36219.8*	***-201.01***
Year *Year^2* *Subpopulation* *Subpopulation*year*		*-0.035* *-0.004*	*0.043* *<0.001*	*35707.98*	***-712.83***
Year *Year^2* *Subpopulation*	*12 km (n=7)*	*0.004* *-0.003*	*0.001* *<0.001*	*36320.17*	***-100.64***
Year		*-0.038*	*0.029*	*36224.1*	***-196.71***

Year² *Subpopulation* *Subpopulation*year*		*-0.004*	*<0.001*		
Year *Year²* *Subpopulation*	*15 km (n=3)*	*0.004* *-0.003*	*0.001* *<0.001*	*36424.28*	*+3.47*
Year *Year²* *Subpopulation* *Subpopulation*year*		*0.004* *-0.003*	*0.001* *<0.001*	*36407.4*	***-13.41***

Figure 2.2a and 2.2b: Great Bustard subpopulations in Extremadura (Spain) and Alentejo (Portugal) defined by buffering adult male observations by 9 km, shown for (a) maximal extent across 1985–2012 (light grey = extant; hatched = extirpated in 2011) derived by dissolving polygons of extent for 1985, 2002 and 2011, (b) separately for 1985 (hatched), 2002 (light grey) and 2011 (black outline). Subpopulation names and abbreviations: 1: Castelo Branco (CBR); 2: Guijo de Coria (GJC); 3: La Mata (LMT); 4: Central Cáceres (CCR); 5: Campo Lugar (CLG); 6: La Serena (SER); 7: Montijo (MTJ); 8: Northern Alentejo–Western Badajoz (NAWB); 9: San Vicente de Alcántara (ALC); 10: Retamal (RTM); 11: Campiña Sur (CMS); 12: Mourão–Villanueva del Fresno (VLF); 13: Evora (EVR); 14: Cuba (CUB); 15: Castro Verde (CVD); 16: Moreanes (MOR).

2.4.2 Subpopulation trends and their regional differences

There were considerable differences in trends between subpopulations. Four—Guijo de Coria, Castelo Branco, Mourão–Villanueva del Fresno and Evora—decreased significantly between 1980 and 2014, while three—Castro Verde, Cuba and Moreanes—increased significantly (Figs. 2.3 and 2.4). The Castelo Branco subpopulation was extirpated by 2000, and the Mourão–Villanueva del Fresno subpopulation is practically extirpated, with two birds counted there in 2014 and zero in 2015. Five of the six largest subpopulations either increased significantly (Castro Verde) or remained stable (Central Cáceres, Northern Alentejo–Western Badajoz, Campiña Sur and Campo Lugar) across the entire study period. Trends of total counts (Fig. 2.3) were visually similar to trends of adult males (Fig. 2.4).

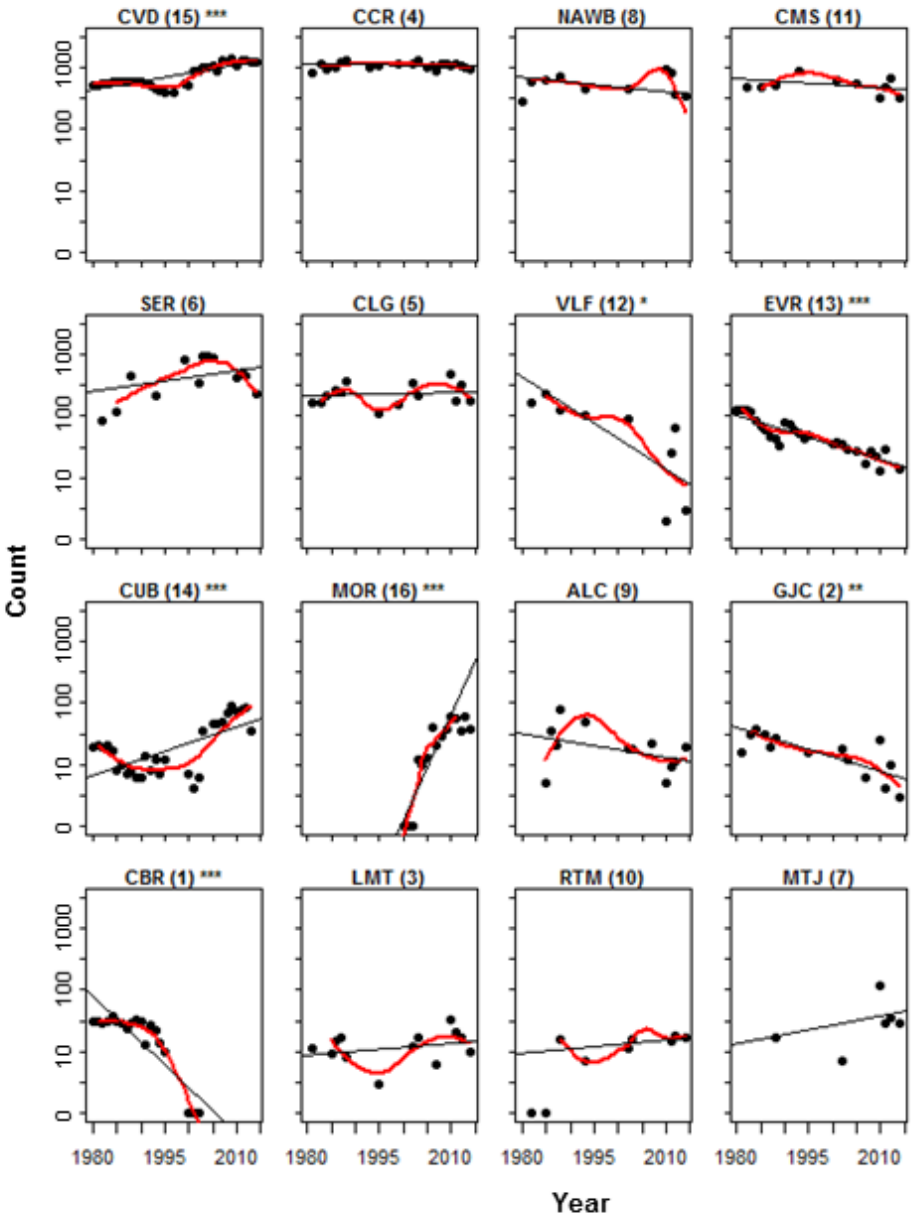


Figure 2.3: Annual counts of total Great Bustard numbers in subpopulations in Extremadura and Alentejo between 1980 and 2014. Abbreviated subpopulation names and numbers refer to Figure 2. Red lines are LOESS models fitted to the count data (black dots); thin black lines are linear regressions relating $\log_{10}$ subpopulation count to year, for which a significant slope is indicated next to the subpopulation name (* $p<0.05$, ** $p<0.01$, *** $p<0.001$). First counts were excluded from LOESS and linear models.

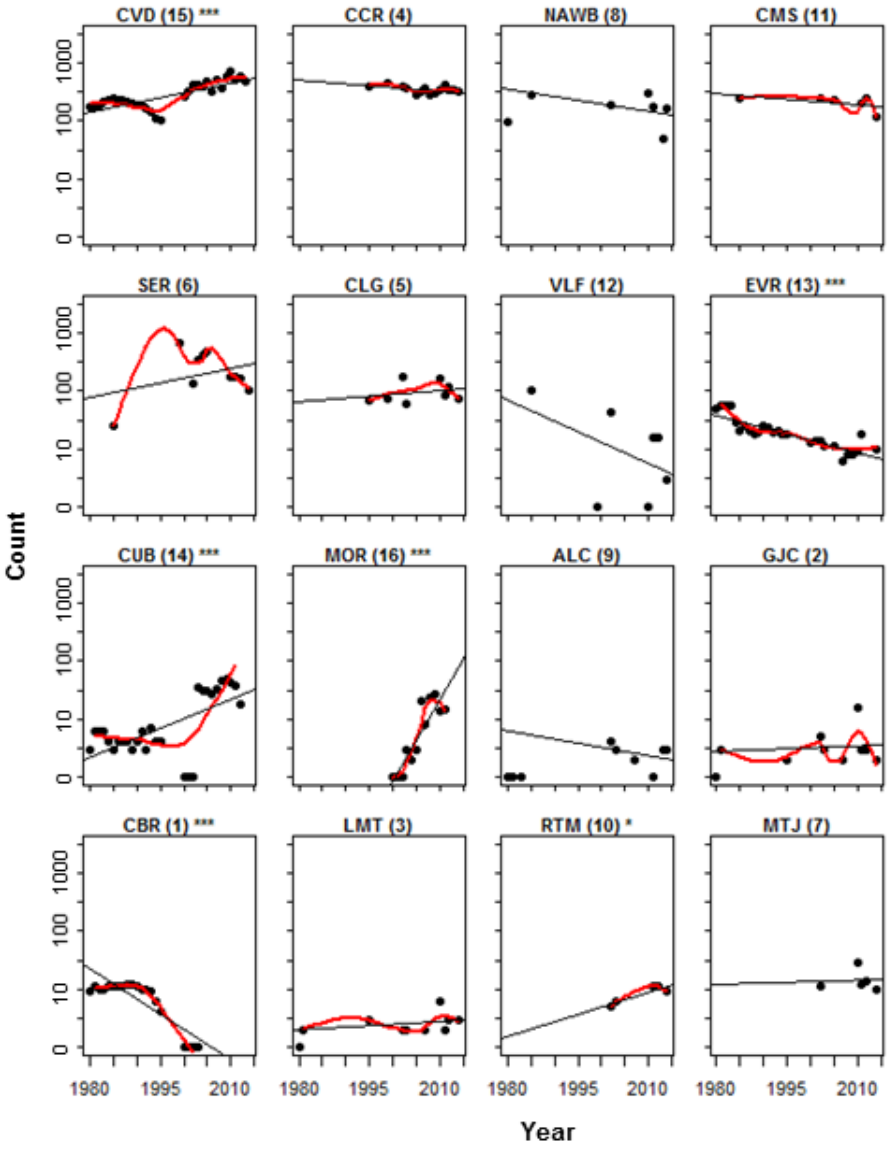


Figure 2.4: Annual counts of adult male Great Bustards in subpopulations in Extremadura and Alentejo between 1980 and 2014. Abbreviated subpopulation names and numbers refer to Figure 2. Red lines are LOESS models fitted to the data (black dots); thin black lines are linear regressions relating $\log_{10}$ subpopulation total count to year, for which a significant slope is indicated next to the subpopulation name (* $p<0.05$, ** $p<0.01$, *** $p<0.001$). First counts were excluded from LOESS and linear models.

Results of GLMs examining temporal trends in total counts of subpopulations between 1980 and 2014 showed strong support for a non-linear trend best explained by a quadratic term, indicating an overall decline from the 1980s into the 1990s, and an increase in the 2000s (Fig. 2.5). The best-supported model also included the interaction between year and subpopulation, confirming different temporal trends among subpopulations (Table 2.3 section A). Total numbers in the region (from the sum of subpopulations) were estimated to be 3,614 (95% CI 3,484–3,747) in 1985, 2,548 (2,414–2,678) in 2002, and 4,610 (4,474–4,712) in 2014. Numbers predicted for the start of the period (1985) were similar to actual counts in that year: 3,417. However, this model did not indicate the recent decline in most of Extremadura and northern Alentejo noted in actual counts (see below), likely due to the short duration of these declines, so that the use of a quadratic term but not higher polynomials was supported in model selection. In 2011 the actual count was 4,783, similar to the end-point prediction of the model (4,610) in 2014, but due to the quadratic structure of the model it did not predict the subsequent decline from 2010 to a total actual count of 3,512 in 2014 (Appendix 2.2). A model that included a cubic term was not better supported based on the change in AICc values (Table 2.3 section A), but estimated a total of 2,956 (2,821–3,087) in 2014, close to the actual number in that year (above).

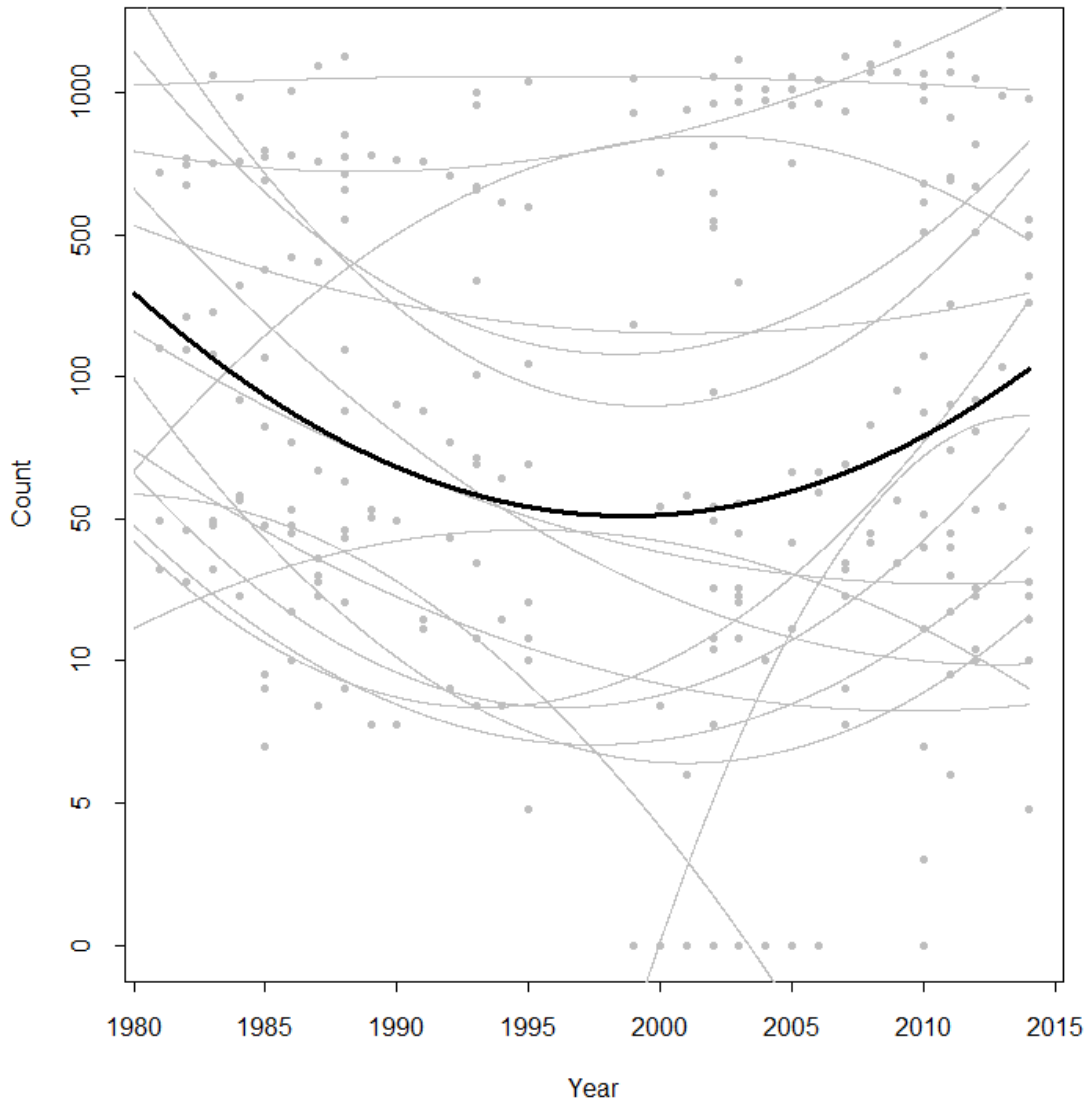


Figure 2.5: Trends of 16 Great Bustard subpopulations (259 annual counts) in Extremadura and Alentejo between 1980 and 2014. Grey points and lines are subpopulation-specific annual counts with fitted GLMs relating $\log_{10}$(subpopulation total +1) to both year and the second-order orthogonal polynomial term of year. Thick black line represents the mean overall trend, based on a GLM relating $\log_{10}$(mean of all predicted subpopulation total +1) to year, a second-order orthogonal polynomial term of year, subpopulation identifier (categorical) and an interaction term between year and subpopulation identifier.

Table 2.3: Results of Gaussian generalised linear models of annual counts of Great Bustards in subpopulations (n = 16 subpopulations, 259 counts, $\log_{10}(n+1)$ transformed) in Extremadura and Alentejo between 1985 and 2014. ΔAICc values of models in section A represent changes in AICc values compared to the null model, those in sections B and C represent changes relative to the best-supported model (in bold) of group A. ΔAICc values in **bold** represent best supported model.

Group	***Model***	***B***	***SE***	***AICc***	***ΔAICc***
A) Models of year (with orthogonal polynomials), subpopulation, and their interactions	*Null model*			*698.72*	*0*
	Year	*-0.002*	*0.006*	*700.62*	*1.9*
	Year *Subpopulation*	*-0.004*	*0.003*	*408.03*	*-290.69*
	Year *Subpopulation* *Year:subpopulation*	*0.075*	*0.298*	*332.30*	*-366.42*
	Year ***Year²*** ***Subpopulation*** ***Year:subpopulation***	***0.075*** ***1.621***	***0.291*** ***0.457***	***320.83***	***-377.89***
	Year *Year²* *Year³* *Subpopulation* *Year:subpopulation*	*0.073* *1.149* *-0.084*	*0.280* *1.729* *0.468*	*328.94*	*-369.78*
	Year *Year²* *Subpopulation* *Year:subpopulation* *Year²:subpopulation*	*0.075* *1.131*	*0.279* *1.722*	*325.85*	*-372.87*
	Year *Year²* *Year³* *Subpopulation* *Year:subpopulation* *Year^²:subpopulation*	*0.073* *1.149* *-0.084*	*0.280* *1.729* *0.468*	*328.94*	*-369.78*
	Year *Year²* *Year³* *Subpopulation* *Year:subpopulation* *Year^³:subpopulation*	*0.106* *0.689* *2.093*	*0.280* *1.766* *2.001*	*356.80*	*-341.92*
	Year *Year²* *Year³* *Subpopulation* *Year²:subpopulation* *Year³:subpopulation*	*0.106* *0.689* *2.093*	*0.280* *1.766* *2.001*	*356.80*	*-341.92*

	Year *Year^2* *Year^3* *Subpopulation* *Year:subpopulation* *Year^2:subpopulation* *Year^3:subpopulation*	*0.106* *0.689* *2.093*	*0.280* *1.766* *2.001*	*356.80*	*-341.92*
B) Add province and interaction	*Year* *Year^2* *Subpopulation* *Province (Alentejo)* *Year:subpopulation* *Year:province*	*0.075* *1.621*	*0.291* *0.457*	*320.83*	*0*
C) Add Castro Verde and interaction	*Year* *Year^2* *Subpopulation* *Castro Verde (no)* *Year:subpopulation* *Year:Castro Verde*	*0.075* *1.621*	*0.291* *0.457*	*320.83*	*0*

No support was found for an overall difference in trends between Extremadura and Alentejo (Table 2.3 section B), or for a difference in trends between Castro Verde (plus the adjacent Cuba and Moreanes) and all other subpopulations (Table 2.3 section C). No support was found for a concentration process within the three largest subpopulations during 1985–2011 (Table 2.4). Recent (2010–2014) subpopulation trends were not affected by the proportion of the subpopulation designated as an SPA (Table 2.5).

Table 2.4: Results of Gaussian generalised linear models predicting proportion (arcsine square-rooted transformed) of Great Bustards in the three largest subpopulations relative to total counts across Extremadura and Alentejo, based on 8 years with complete counts. df shows model error degrees of freedom; ΔAICc represents the change in AICc compared to the null model; **bold** represents strong support.

Model	***df***	***B***	***SE***	***AICc***	***ΔAICc***
Null	***7***			***-16.44***	***0***
Year	*6*	*0.004*	*0.002*	*-16.68*	*-0.22*

Table 2.5: Results of Gaussian generalised linear models relating linear temporal trends of $\log_{10}(1+n)$ counts for 15 subpopulations between 2010 and 2014, to the proportion (arcsine-square rooted) of subpopulation area designated as SPA. df shows model error degrees of freedom; ΔAICc represents the change in AICc compared to the null model; **bold** represents strong support.

Model	***df***	***B***	***SE***	***AICc***	***ΔAICc***
Null	***14***			***-15.73***	***0***
SPA	*13*	*0.028*	*0.119*	*-12.61*	*3.12*

TRIM analysis revealed an overall non-significant negative linear trend across the study period (Wald chi-square (1, df=2)= 1.690, p=0.429; Figure 2.6), and no significant effect of SPA declaration on trends (Wald chi-square (1, df=1)= 1.484, p=0.223).

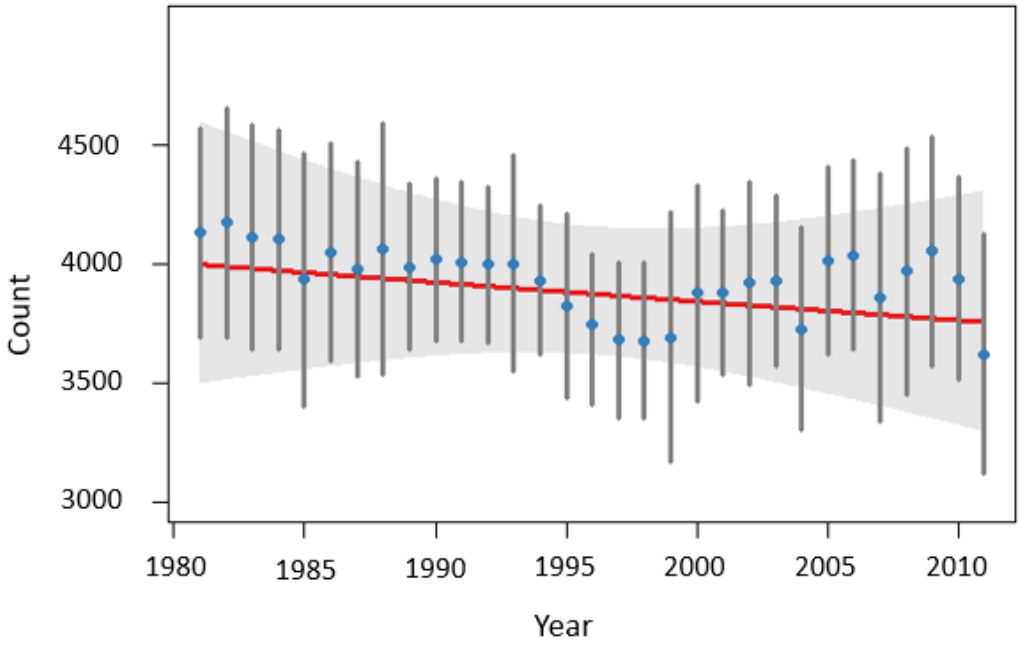


Figure 2.6: TRIM analysis of overall trends of Great Bustards in Extremadura and Alentejo between 1980 and 2015. Red line is the overall linear trend. Blue circles are the annual estimates and SE (grey vertical lines). Shaded grey area is 95% confidence intervals.

2.4.3 Recent decline in Great Bustard numbers

Despite the general increase in the numbers of Great Bustards recorded in actual counts and in model estimates from the early 1980s to recent years, from 2010 onwards actual counts declined in 13 subpopulations of the 15 viable subpopulations in the region (excluding extirpated Castelo Branco). Between 2010 and 2014, count totals declined from 4,966 to 3,512. The total actual count in Extremadura and the northern section of Alentejo decreased from 3,656 in 2010 to 2,244 in 2014. In Badajoz province, the total count (excluding cross-border subpopulations) decreased from 1,666 in 2010 to 821 in 2015. These results indicate negative trends in several subpopulations: in La Serena in eastern Badajoz, counts dropped steeply from 945 in 2004, to 501 in 2011, and to only 426 in 2015; in Central Cáceres, counts dropped from 1227 in 2010 to 768 in 2015. In Northern Alentejo–Western Badajoz, counts dropped from 1,035 in 2010 to 354 in 2014. Counts in both small peripheral subpopulations in northern Cáceres—Guijo de Coria and La Mata—also dropped, from 56 in 2010 to only 11 in 2014.

2.5 Discussion

2.5.1 Updated estimates of Great Bustard numbers in Extremadura and Alentejo

Great Bustard numbers fluctuated considerably in Extremadura and Alentejo between 1985 and 2014, with an initial decline in the 1990s followed by a recovery in the 2000s, the latter driven particularly by population growth at Castro Verde, from 520 in 2000 to 1,482 in 2009 (Fig. 2.5). Alonso (2014) suggested that a ban on hunting in Spain in 1980 caused numbers to rise in the 1980s, but also that improvements in census methodology contributed to higher counts (so some of the 'recovery' may not have been real). The predicted overall decline in the 1990s based on the selected GLM was not apparent in actual counts.

The total regional count of 3,512 Great Bustards in 2014 is 52–58% lower than the previous published totals (see below) — put at 7,393–8,393 by combining the estimate for Extremadura in 2003 (Corbacho *et al.* 2005) with the census data for Alentejo in 2009 (Alonso and Palacín 2010) —and reduces the estimated Iberian population from 31,263–36,163 (Alonso & Palacín 2010) to roughly 28,000–32,000. In 2015 only 2,319 birds were counted in Extremadura, far lower than the previous published estimates by Corbacho *et al.* (2005) of 5,500–6,500 for 2003.

Between 2010 and 2014/5 a decrease in observed numbers in several large and medium-sized subpopulations in Extremadura and northern Alentejo indicates a potential decline in parts of the region (Appendix 2.2). However, this decline in observed numbers is probably too recent to alter the shape of the fitted temporal GLM across the study period, with the best-supported model incorporating a quadratic but lacking the cubic term required to describe this recent downturn. This

decline seems to have driven the overall non-significant TRIM linear trend (figure 2.6). Additionally, it may be that this drop in observed numbers does not represent true population declines, but is a result of a systematic failure to count birds effectively. However, it must be noted that during this period several other agro-steppe bird populations in Iberia have shown similar declines (Silva *et al.* 2018, Palacín & Alonso 2018, de Juana 2009), supporting the suggestion here that a dramatic decline in Great Bustard numbers is occurring in Extremadura and Alentejo.

2.5.2 Subpopulations and their trends

Trends in subpopulations across the region show two interesting patterns. First, as noted above, five of the six largest subpopulations either increased significantly or did not change significantly during the entire study period, reinforcing the notion that large subpopulations may be more resilient to declines (Alonso *et al.* 2004). Second, increases in the two small subpopulations in the southern Alentejo adjacent to Castro Verde (Cuba and Moreanes) are possibly linked to the parallel increase in Castro Verde, and may represent a 'spillover' from it, though there is no direct evidence for this yet.

The concentration process at Castro Verde, Cuba and Moreanes suggested by Pinto *et al.* (2005) stalled later in the study period. Numbers at this subpopulation levelled off or even decreased slightly during 2010–2014, and numbers in other large subpopulations also failed to increase.

2.5.3 Definition of subpopulations – methodological considerations

Use of spring counts in this study resulted in substantially lower figures than previous estimates based on winter counts (Alonso *et al.* 2003; Corbacho *et al.* 2005). Alonso *et al.* (2003) and Corbacho *et al.* (2005) suspected that spring counts underestimate the numbers of females and consequently regarded the higher winter counts as more reliable. Conversely, estimates of breeding numbers based on winter counts are considered here more likely to be inflated. Winter count totals in Extremadura were on average 86% higher (n = 10, range 17–212 %, SD 56 %) than corresponding spring counts (Corbacho *et al.* 2005). Additionally, comparison of subpopulation trends using spring and winter counts suggested that trends were different between seasons, indicating that numbers in winter are augmented by birds from external sources (Appendix 2.3). Such higher winter numbers may result at least partly from immigration from breeding populations, as far as 200–300 km away (Alonso *et al.* 2005). Great Bustards can migrate over long distances (Palacín *et al.* 2009; Kessler *et al.* 2013), and wintering sites in Cáceres are both lower (c. 400 m a.s.l.) and warmer (1961–1990: January mean minimum daily temperature 7.9°C) than major breeding sites near Salamanca, Castilla y Leon (c. 800 m a.s.l., mean 3.6°C) (Meteorologisk Institutt 2017). Moreover, Great Bustards are probably more mobile in winter, increasing the risk of double-counting.

By contrast, any underestimation of females in spring counts will have been modest, for several reasons. (1) The census methods in the region conform, as noted above, with principles formalised by Alonso *et al.* (2005), and carried out by professional teams that have full access even to private areas. Acknowledging the potential limitations of spring census data, i.e. the potential to undercount females,

and the variability in identification skills among teams, I evaluate these spring count data as still valid (2) I base my approach on the analysis of long-term trends rather than individual counts. (3) Trends of adult males are visually consistent with trends of total counts. Adult males are conspicuous, aggregate in focal areas during the study period before 'lek explosion' (Alonso, Álvarez-Martínez & Palacín 2012), and are unlikely to be underestimated. If female numbers were significantly underestimated, different trends between total counts and adult males would be expected, but are not evident (Figs. 2.3 and 2.4).

It is acknowledged, however, that the spatial movement data used in this study come from Great Bustard populations that are relatively stable or increasing (e.g. Alonso *et al.* 2009; Magaña *et al.* 2011), from different parts of Iberia, and from some years ago. Potentially, climatic differences and other environmental and biological factors (including dramatic demographic changes) may cause birds in Extremadura and Alentejo to use space and habitat in different ways to other parts of Iberia.

2.5.4 Conservation implications

The overall increase in numbers in SPA Castro Verde (Pinto *et al.* 2005) and adjacent Moreanes is probably the result of successful agri-environmental schemes in these areas (Santana *et al.* 2014), that may have also provided a source for numbers in Cuba. However, we found no link between subpopulation trends and SPA declaration, although this may partly reflect our use of a simplified metric to rank SPA effectiveness. Indeed, several recently declining subpopulations include large areas designated as SPAs: La Serena, Campiña Sur, Evora, Mourão–Villanueva de Fresno, and most of the Alentejo section of the Northern Alentejo–Western Badajoz subpopulation. This raises concerns about the performance of SPAs in protecting agro-steppe habitats and bird species, and suggests that some subpopulations might benefit from greater coordination of management between Spain and Portugal. With better information on actual conservation activities on the ground, function of the SPA network across Extremadura and Alentejo in protecting agro-steppe birds needs to be studied more thoroughly.

Agricultural systems are intensifying over large parts of the region, and are believed to be negatively affecting Great Bustards and other steppe bird species (Corbacho *et al.* 2005; Sánchez and Garcia-Baquero 2012; Pinto *et al.* 2005; Santana *et al.* 2014). Land-use and infrastructural changes affect reproduction rates, mortality rates and recruitment in Great Bustards (Martín *et al.* 2007; Raab *et al.* 2010, 2011; Rocha *et al.* 2012). The recent declines observed in so many Great Bustard subpopulations indicating an overall population decline, require the urgent need to understand the reasons for these potential declines that are still unstudied. It is imperative to confirm (and then decisively counter) the link between Great

Bustard declines in Extremadura and Alentejo and land-use and infrastructural intensification, that may be the main drivers for declines of agro-steppe birds.

2.6 Acknowledgements

We thank all staff and volunteers who participated in Great Bustard counts in Alentejo and Extremadura, and express our special gratitude to Joaquín Dávalos, Junta de Extremadura, for his assistance in obtaining and interpreting long-term Great Bustard count data. Funds supporting JH's census work were provided by World Wildlife Fund Spain. Agustín Mogena helped obtain data from Llanos de Cáceres, and participated in fieldwork. YP was funded by a Lord Zuckerman Studentship 2014–2018 and by the Kenneth Lindsay Scholarship Trust.

2.7 References

Alonso, J.C. (2014) The great bustard: past, present and future of a globally threatened species. *Ornis Hungarica*, **22***, 1–13.*

Alonso, J.C., Alonso, J.A., Martín, C.A., Palacín, C., Magaña, M. & Martín, B. (2005) Los censos de avutardas: aspectos metodológicos. *La Avutarda Comun en la Peninsula Iberica: Poblacion Actual y Metodo de Censo* (eds J.C. Alonso, C. Palacín, & C.A. Martín), p. SEO/BirdLife, Madrid.

Alonso, J.C., Martín, E., Alonso, J.A. & Morales, M.B. (1998) Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. *Behavioral Ecology*, ***9****, 243–252.*

Alonso, J.C., Morales, M.B. & Alonso, J.A. (2000) Partial migration, and lek and nesting area fidelity in female great bustards. *Condor*, **102***, 127–136.*

Alonso, J.C., Palacín, C. & Martín, C.A. (2003) Status and recent trends of the great bustard (*Otis tarda*) population in the Iberian peninsula. *Biological Conservation*, **110***, 185–195.*

Alonso, J.C., Martín, C.A., Alonso, J.A., Palacín, C., Magaña, M. & Lane, S.J. (2004) Distribution dynamics of a great bustard metapopulation throughout a decade: influence of conspecific attraction and recruitment. *Biodiversity and Conservation*, **13***, 1659–1674.*

Alonso, J.C., Palacín, C. & Martín, C.A. (2005) Censo y distribución de avutardas en la península Ibérica. *La Avutarda Comun en la Peninsula Iberica: Poblacion Actual y Metodo de Censo* (eds J.C. Alonso, C. Palacín, & C.A. Martín), pp. 8–13. SEO/BirdLife, Madrid.

Alonso, J.C., Palacín, C., Alonso, J.A. & Martín, C.A. (2009) Post-breeding migration in male great bustards: low tolerance of the heaviest Palaearctic bird to summer heat. *Behavioral Ecology and Sociobiology*, **63***, 1705–1715.*

Alonso, J.C. & Palacín, C. (2010) The world status and population trends of the great bustard (*Otis tarda*): 2010 update. *Chinese Birds*, **1***, 141–147.*

Alonso, J.C., Álvarez-Martínez, J.M. & Palacín, C. (2012) Leks in ground-displaying birds: hotspots or safe places? *Behavioral Ecology*, **23**, 491–501.

Bartoń, K. (2013) MuMIn: multi-model inference, R package version 1.9.13.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) lme4: Linear mixed-effects models

using Eigen and S4, R package version 1.1-8. Downloaded from http://cran.r-project.org/package=lme4.

BirdLife International (2018) Species factsheet: *Otis tarda*, http://www.birdlife.org/datazone/ [accessed 10 October 2017]

Bogaart, P., van der Loo, M., & Panekoek, J. (2018). rtrim: Trends and Indices for Monitoring Data. R package version 2.0.6. Retrieved from https://cran.r-project.org/package=rtrim

Bright, J.W. & Dawkins, C.S. (1965) Some aspects of curve fitting using orthogonal polynomials. *Industrial and Engineering Chemistry Fundamentals*, **4***, 93–97.*

Burnham, K.P. & Anderson, R.P. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33***, 261–304.*

Cleveland, W.S. & Devlin, S.J. (1988) Locally weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association*, **83***, 596–610.*

Collar, N.J. (1985) The world status of the great bustard. *Bustard Studies*, **2***, 1–20.*

Collar, N., & Garcia, E. F. J. (2018). Great Bustard (*Otis tarda*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions.

Collar, N.J. (1991) Red Data Book; Great bustard. *World Birdwatch*, **13**.

Corbacho, C., Fernández, E., Costillo, E., Lozano, A. & Gil, A. (2005) La avutarda común en Extremadura: distribución, población y tendencias. *La Avutarda Comun en la Peninsula Iberica: Poblacion Actual y Metodo de Censo* (eds J.C. Alonso, C. Palacín, & C.A. Martín), pp. 34–43. SEO/BirdLife, Madrid.

ESRI (2014) ArcMap. Version 10.2.2. Environmental Systems Research Institute. Redlands, California.

European Commission (2017) Natura 2000, http://ec.europa.eu/environment/nature/natura2000/ [accessed 10 October 2017]

Faragó, S., Spakovszky, P., & Raab, R. (2014). Conservation of Great Bustard (*Otis tarda*) population of the Mosoni-Plain - a success story. *Ornis Hungarica*, **22**, 14–31. doi:10.2478/orhu-2014-0015

Kessler, A.E., Batbayar, N., Natsagdorj, T., Batsuur', D. & Smith, A.T. (2013) Satellite telemetry reveals long-distance migration in the Asian great bustard *Otis tarda*

dybowskii. *Journal of Avian Biology*, **44***, 311–320.*

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.

Magaña, M., Alonso, J.C., Alonso, J. A., Martín, C.A., Martín, B. & Palacín, C. (2011) Great bustard (*Otis tarda*) nest locations in relation to leks. *Journal of Ornithology*, **152***, 541–548.*

Martín, C.A., Alonso, J.C., Alonso, J.A., Palacín, C., Magaña, M. & Martín, B. (2007) Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard *Otis tarda*. *Journal of Avian Biology*, **38***, 335–346.*

Martín, C.A., Alonso, J.C., Alonso, J.A., Palacín, C., Magaña, M. & Martín, B. (2008) Natal dispersal in great bustards: the effect of sex, local population size and spatial isolation. *Journal of Animal Ecology*, **77***, 326–334.*

Martín, C.A., Alonso, J.C., Alonso, J.A., Pitra, C. & Lieckfeldt, D. (2002) Great bustard population structure in central Spain: concordant results from genetic analysis and dispersal study. *Proceeding of the Royal Society B: Biological Sciences*, **269***, 119–125.*

Meteorologisk Institutt (2017) http://www.yr.no/ [accessed 10 October 2017]

Morales, M.B., Alonso, J.C., Alonso, J.A. & Martín, E. (2000) Migration patterns in male great bustards (*Otis tarda*). *Auk*, **117***, 493–498.*

Nagy, S. (2009) *International Single Species Action Plan for the Western Palearctic Population of Great bustard, Otis tarda tarda.* BirdLife International.

Oparin, M. L., Oparina, O. S., Kondratenkov, I. A., Mamaev, A. B., & Piskunov, V. V. (2013). Factors causing long-term dynamics in the abundance of the Trans-Volga great bustard (*Otis tarda L.*) population. *Biology Bulletin*, **40**, 843–853. doi:10.1134/S1062359013100063

Palacín, C. & Alonso, J.C. (2008) An updated estimate of the world status and population trends of the great bustard *Otis tarda*. *Ardeola*, **55***, 13–25.*

Palacín, C., Alonso, J.C., Alonso, J.A., Martín, C.A., Magaña, M. & Martin, B. (2009) Differential migration by sex in the great bustard: Possible consequences of an extreme sexual size dimorphism. *Ethology*, **115***, 617–626.*

Palacín, C., Alonso, J. C., Martín, C. A., & Alonso, J. A. (2016). Changes in bird-migration

patterns associated with human-induced mortality. *Conservation Biology*, **31**, 106–115. doi:10.1111/cobi.12758

Pinto, M., Rocha, P. & Moreira, F. (2005) Long-term trends in great bustard (*Otis tarda*) populations in Portugal suggest concentration in single high quality area. *Biological Conservation*, **124***, 415–423.*

Plieninger, T. (2006) Habitat loss, fragmentation, and alteration – quantifying the impact of land-use changes on a Spanish Dehesa landscape by use of aerial photography and GIS. *Landscape Ecology*, **21***, 91–105.*

Raab, R., Spakovszky, P., Julius, E., Schütz, C. & Schulze, C.H. (2010) Effects of power lines on flight behaviour of the West-Pannonian great bustard *Otis tarda* population. *Bird Conservation International*, **21***, 142–155*.

Raab, R., Schütz, C., Spakovszky, Pét., Julius, E. & Schulze, C.H. (2011) Underground cabling and marking of power lines: conservation measures rapidly reduced mortality of West-Pannonian great bustards *Otis tarda*. *Bird Conservation International*, **22***, 299–306.*

Raab, R., Kollar, H. P., Winkler, H., Faragó, S., Spakovszky, P., Chavko, J., … Schütz, C. (2010). Development of the West Pannonian population of the Great Bustard, *Otis tarda* Linnaeus 1758,from 1900 to the winter 2008/2009. *Egretta*, **51**, 74–99.

R Core Team (2017) R: A language and environment for statistical computing, version 1.1.383, http://www.r-project.org/.

Richards, S.A. (2008) Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, **45***, 218–227.*

Rocha, P. (2006) *Dinâmica Populacional E Distriuição Da Abetarda No Baixo-Alentejo - Relação Com O Uso Da Terra*. PhD thesis. University of Lisbon, Portugal.

Rocha, P., Morales, M.B. & Moreira, F. (2012) Nest site habitat selection and nesting performance of the great bustard *Otis tarda* in southern Portugal: Implications for conservation. *Bird Conservation International*, **23***, 323–336.*

Sánchez, A. & Garcia - Baquero, M.J. (2012) La avutarda en Badajoz: Estabilidad, pero con matices. *Quercus*, **314***, 16–22.*

Santana, J., Reino, L., Stoate, C., Borralho, R., Carvalho, C.R., Schindler, S., Moreira, F., Bugalho, M.N., Ribeiro, P.F., Santos, J.L., Vaz, A., Morgado, R., Porto, M. & Beja, P.

(2014) Mixed effects of long-term conservation investment in Natura 2000 farmland. *Conservation Letters*, **7**, *467–477.*

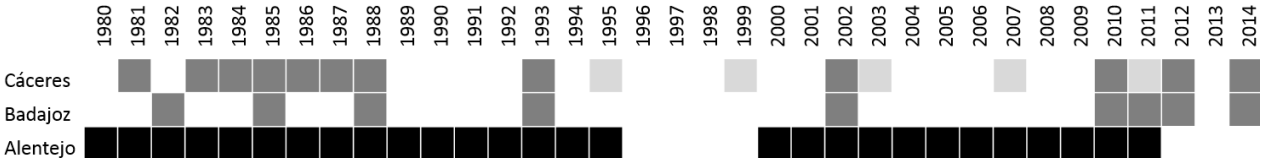
Schwandner, J., & Langgemach, T. (2011). How much habitat is left for the great bustard (*Otis tarda*)? Human infrastructure and remaining suitable habitat in western Brandenburg (Germany). *Berichte Zum Vogelschutz*, **47**, 193–206.

van Strien, A., Pannekoek, J., Hagemeijer, W., & Verstrael, T. (2004). A loglinear poisson regression method to analyse bird monitoring data. *Bird Census News*, **13**, 33–39.

Appendices

Appendix 2.1: Great Bustard spring count data between 1980 and 2014 provided for this study.

Black boxes are data provided ICNF, dark grey boxes are data provided by Junta de Extremadura, and light grey boxes are data provided by WWF / J. Hellmich.



Appendix 2.2: Subpopulation total counts in Extremadura (Spain) and Alentejo (Portugal) 1980 – 2015.

Year	*Gujo de Coria*	*La Mata*	*Castelo Branco*	*Central Cáceres*	*Campo Lugar*	*La Serena*	*Retamal*	*Campiña Sur*	*San Vicente de Alcantara*	*N Alentejo - W Badajoz*	*Montijo*	*Mourão–Villanueva del Fresno*	*Evora*	*Cuba*	*Moreanes*	*Castro Verde(total)*	*Castro Verde (core)*
1980			*29*										*126*	*18*		*516*	*513*
1981	*15*	*5*	*30*	*803*	*168*								*126*	*20*		*523*	*521*
1982			*28*			*84*		*638*		*517*		*161*	*124*	*18*		*555*	*555*
1983	*30*		*29*	*1148*	*168*								*119*	*20*		*567*	*567*
1984	*37*		*30*	*969*	*209*								*82*	*16*		*574*	*574*
1985	*22*	*8*	*29*	*1033*	*220*	*114*		*549*	*4*	*535*		*237*	*66*	*7*		*593*	*593*
1986	*29*	*14*	*27*	*1013*	*262*				*33*				*58*	*9*		*601*	*601*
1987	*18*	*16*	*22*	*1247*	*253*				*19*				*46*	*6*		*573*	*573*
1988	*26*	*7*	*28*	*1348*	*359*	*454*	*15*	*554*	*75*	*815*	*17*	*134*	*42*	*7*		*597*	*597*
1989			*31*										*33*	*5*		*600*	*600*
1990			*30*										*79*	*5*		*580*	*580*
1991			*12*										*75*	*13*		*570*	*570*
1992			*26*										*58*	*7*		*512*	*512*
1993			*21*	*999*		*218*	*6*	*954*	*48*	*454*		*101*	*51*	*11*		*465*	*465*
1994			*13*										*43*	*6*		*413*	*413*
1995	*15*		*9*	*1096*	*110*								*48*	*11*		*393*	*393*
1996																	
1997																*398*	*398*
1998																	
1999				*1127*	*151*	*859*										*562*	*562*
2000													*34*	*6*		*520*	*520*
2001													*37*	*3*		*870*	*870*
2002	*13*	*11*		*1197*	*323*	*303*	*10*	*812*	*31*	*470*	*7*	*56*	*34*	*5*		*1043*	*912*
2003	*11*			*1304*	*215*	*929*	*10*		*17*				*27*	*35*	*11*	*1089*	*1043*

Year	*Guijo de Coria*	*La Mata*	*Castelo Branco*	*Central Cáceres*	*Campo Lugar*	*La Serena*	*Retamal*	*Campiña Sur*	*San Vicente de Alcantara*	*N Alentejo - W Badajoz*	*Montijo*	*Mourão–Villanueva del Fresno*	*Evora*	*Cuba*	*Moreanes*	*Castro Verde(total)*	*Castro Verde (core)*
2004						*945*									*9*	*1032*	*1032*
2005				*1163*		*907*		*565*					*25*	*45*	*12*	*1134*	*1093*
2006				*1106*										*45*	*38*	*912*	*873*
2007	*5*	*5*		*1378*					*21*				*16*	*48*	*20*	*1340*	*1297*
2008				*1180*									*25*	*67*	*27*	*1259*	*1212*
2009				*1176*									*21*	*89*	*36*	*1482*	*1410*
2010	*24*	*32*		*1227*	*481*	*412*		*323*	*4*	*1035*	*118*		*12*	*74*	*61*	*1163*	*1048*
2011	*3*	*19*		*1163*	*179*	*501*	*16*	*491*	*8*	*832*	*27*	*24*	*27*	*79*	*54*	*1360*	*1300*
2012	*9*	*16*		*1333*	*322*	*465*	*17*	*658*	*10*	*369*	*33*	*63*		*82*	*35*		*1348*
2013				*980*										*34*	*58*		*1230*
2014	*2*	*9*		*1076*	*181*	*226*	*16*	*332*	*18*	*354*	*28*	*2*	*13*		*37*		*1218*
2015				*768*	*214*	*426*		*395*		*516*							

Appendix 2.3: Comparison between trends in winter and spring counts

To test if trends in winter subpopulation counts are different from trends in spring subpopulation counts, we used data published in Corbacho *et al.* (2005) that includes spring and winter subpopulations counts in Extremadura between 1981 and 2002. Junta de Extremadura stopped winter counts in 2003 across Extremadura. Additionally, for this analysis we used data provided by Agustín Mogena with spring and winter counts in ZEPA Llanos de Cáceres only between 2003 and 2013. Winter counts were never carried out in Alentejo. 133 winter counts and 69 spring counts of 10 subpopulations were used in the analysis.

Using generalized linear models with negative binomial error distribution (selected based on residual deviance/df= 1.17; Gaussian, log(n+1)= 0.12; Gaussian, sqrt = 40.57; Gaussian, raw= 118376.54; Poisson= 144.48), year-specific subpopulation counts were related to year, subpopulation ID (factor) and interaction term between year and subpopulation ID. To this model, season of count was added as factor (winter is additive effect, spring is reference level) as well as the interaction term between year and season, to create models with seasonal differences between trends. Models were compared based on changes in AICc, and was considered to be strongly supported if AICc values reduced by >2 (Burnham & Anderson 2004)

Results of the comparison between the models support the seasonal difference between trends of subpopulations, with alternative models that do not include season as a predictor not receiving significant support (ΔAICc=39.13; Table A2.3.1).

Table A2.3.1: Results of generalised linear models relating year-specific subpopulation counts in Extremadura between 1981 and 2002, and in ZEPA Llanos de Cáceres only between 2003 and 2013, and season of count (spring or winter). ΔAICc value is change in AICc values between basic model and developed models that included season. **Bold** indicates strong support.

Model	***B***	***SE***	***AICc***	***ΔAICc***
Year *Subpopulation ID* *Subpopulation ID : year*	*0.003*	*0.075*	*2574.46*	*0*
Year *Subpopulation ID* *Subpopulation ID : year* *Season (winter)*	*0.009* *0.605*	*0.029* *0.085*	*2536.41*	*-38.05*
Year *Subpopulation ID* *Subpopulation ID : year* *Season (winter)* *Season : year*	*0.019* *40.804* *-0.020*	*0.029* *19.859* *0.010*	*2535.33*	***-39.13***

Chapter 3

Declines in Great Bustard subpopulations across Extremadura (Spain) and Alentejo (Portugal) may be related to increases in livestock densities

3.1 Abstract

In Iberia, an important region for farmland and grassland birds, agricultural systems are intensifying, yet long-term studies linking landscape-scale agricultural changes to changes in populations of Iberian farmland birds are few. For this study, monitoring data on Great Bustards in Extremadura (Spain) and Alentejo (Portugal) between 1980 and 2014 were used alongside open-access agricultural databases to examine links between changes in Great Bustard numbers and agricultural practices. Across the study area, extent of habitats important to Great Bustards changed during the period for which land-use data were available (1990 to 2012declined. During the period for which livestock data were available (1989–2009), densities of sheep-plus-goats increased markedly across the study area in 12 subpopulations and densities of cattle increased in 3 subpopulations. Using generalised linear models, annual geometric growth rates (trends) of 15 Great Bustard subpopulations were related to changes in the extent of different agro-steppe land-cover types across three discrete time periods (1990 to 2000, 2000 to 2006, 2006 to 2012). In separate generalised linear models, subpopulation trends across two discrete time periods (1989 to 1999, 1999 to 2009) were related to changes in densities of (1) cattle (dairy and beef), (2) sheep and goats combined, and (3) Livestock Units (LSU). No support was found that trends in Great Bustard subpopulations were related to long-term changes in the extent of different land-use classes (n=43 changes). Strong support was found that trends of Great Bustard subpopulations were negatively related to long-term increases in LSU density in subpopulations (n =18 changes). The results suggest that management of livestock at landscape scales had stronger links with Great Bustard trends than moderate

changes in the extent of different land-uses. To protect Great Bustards, key habitat types should be protected from extreme changes, and livestock densities should not increase.

3.2 Introduction

Anthropogenic land-use changes such as agricultural intensification, urbanisation and infrastructure development have generated considerable biodiversity loss globally (e.g. Pimm & Raven 2000; Foley *et al.* 2005; Green *et al.* 2005; Jetz, Wilcove & Dobson 2007). Agricultural intensification has caused declines in farmland birds in Iberia (Díaz, Naveso & Rebollo 1993; Stoate, Borralho & Araújo 2000), the United Kingdom (Chamberlain *et al.* 2000; Chamberlain & Fuller 2000) and elsewhere in Europe (Donald *et al.* 2006; Wretenberg *et al.* 2006; Reif *et al.* 2008; Berg *et al.* 2015). More specifically, breeding farmland birds may be negatively affected by the intensification of agricultural practices, including loss of landscape elements, development of irrigation systems, higher application of fertilizers, herbicides, fungicides and pesticides, and increases of livestock densities, leading to loss and degradation of habitats for breeding birds (Kamp *et al.* 2015, Geiger *et al.* 2010). Intensification of livestock densities on pastoral land may have strong effects on ground-breeding birds that use these systems for breeding. The effects of livestock grazing on farmland and grassland birds vary spatially and between bird species. In Portugal, several grassland species showed mixed responses to different levels and types of livestock grazing – Short-toed Lark *Calandrella brachydatyla* favoured higher grazing intensity, mainly by sheep, and Corn Bunting *Emberiza calandra* favoured taller grass in cattle pastures, as did Little Bustards *Tetrax tetrax* (Reino *et al.* 2010).

In Iberia, several farmland and steppe bird species are declining, and classified as endangered both globally Endangered, e.g. Great Bustard *Otis tarda*

(VU) and Little Bustard (NT), (BirdLife International 2018), and threatened in Europe, e.g. Black-bellied Sandgrouse *Pterocles orientalis* (EN), Little Bustard (VU) and Dupont's Lark *Chersophilus duponti* (VU) (BirdLife International 2015). Additionally, 11 Iberian farmland bird species that appear in Annex 1 of the European Union Birds Directive 2009/147/EC are of conservation concern in Europe. In Iberia, changes in agricultural practices have apparently had considerable consequences on farmland birds. Traditional agricultural practices are giving way to modern practices: Agro-pastoral three- or four-year rotational systems of dry cereals, mainly barley and wheat with fallow periods and sheep grazing, of great importance for Iberian farmland birds, have been partially replaced with more economically favourable agricultural schemes, such as irrigated and permanent crops, and have partially lost their rotation cycles (Suarez, Naveso & De Juana 1997; Correal *et al.* 2003). Furthermore, livestock grazing has expanded its area in southern Portugal between 2000-2002 and 2008-2010 by 34% (cattle grazing) and 50% (sheep grazing) (Ribeiro *et al.* 2014), and landscape heterogeneity has reduced (Suárez, Naveso & De Juana 1997, Cabanillas, Aliseda & Gallego 2012, Martín *et al.* 2012a). Alongside increases in cattle densities, the area used to produce hay and silage in Iberia has increased (e.g. 34% increase of the surface of the main crops used for haying in southern Portugal: data from www.ine.pt in Faria, Morales & Rabaça 2016b). In hay fields, extremely high rates of nest destruction were recorded (Green *et al.* 1997; Grüebler *et al.* 2008; Faria, Morales & Rabaça 2016a; b).

Understanding how landscape-scale agricultural processes affect threatened species might aid conservation managers to plan sustainable agricultural systems

that better support biodiversity, e.g. conservation interventions through agri-environmental schemes (Batáry *et al.* 2011). However, detailed long-term studies that link changes in agricultural practices to changes in the conservation status of Iberian farmland birds are few, despite the importance of Iberia to threatened farmland birds, and the widespread processes of agricultural intensification in both Spain and Portugal. The Great Bustard is one of the most-studied species of the Iberian grasslands (see summary of current knowledge in Alonso 2014). However, even for this charismatic species, large-scale long-term responses to agricultural intensification have not yet been studied. Martín *et al.* (2012) showed a positive correlation between local development of non-irrigated legume cultivation and provincial increases of Great Bustards in northwestern Spain. Increase in irrigation schemes and permanently irrigated crops, decrease in non-irrigated arable land, and increase in livestock densities in pastoral systems have been suggested as causes of declines and extirpation of Great Bustards in multiple studies in southwestern Iberia, but these hypotheses have not been tested (e.g. Corbacho *et al.* 2005; Sánchez & Garcia-Baquero 2012; Santana *et al.* 2014). Pinto *et al.* (2005) showed several significant changes in the extent of those land-uses that are associated with Great Bustards in Alentejo, Portugal, but did not explicitly seek to relate changes in agricultural practices to changes in Great Bustard numbers.

Extremadura (Spain) and Alentejo hold 15–17% (see Chapter 2) or 20-27% (based on older published totals, (Alonso & Palacín 2010) of the Iberian Great Bustard population, in a complex scenario of mixed trends of local increases and decreases (see Chapter 2). Therefore, it is important to understand whether and which changes in agricultural practices in Extremadura and in Alentejo contribute to

trends in the species. With this work I specifically aim to relate long-term monitoring data on Great Bustards to lanscape-scale agricultural data from Extremadura and the Alentejo, to test whether trends in Great Bustard numbers are linked with landscape-scale changes in the extent of different land-uses. Based on information detailed above, I predict that Great Bustards respond negatively to intensification of agricultural systems, more specifically to changes in the extent of favourable and non-favourable land-uses, and changes in livestock densities. Great Bustard is a slow-reproducing species: females settle at their first breeding site at an age of two or three years, while males join their first lek (display congregation of males) at the age of two to four years (Alonso *et al.* 1998). After their first year of life, mortality rates are below 10% (Martín *et al.* 2007). Lagged demographic responses to environmental conditions were shown in Scottish Northern Fulmars *Fulmarus glacialis*, another long-lived bird (Thompson & Ollason 2001). Therefore, it is predicted that demographic trends caused by land-use changes, specifically decreases in breeding productivity, become apparent after a lagged period of approximately six years, based on the age of sexual maturity of Great Bustard (Alonso *et al.* 2004). In this study I test whether lagged responses of subpopulation trends to land-use changes do occur.

I also predict that the composition of different components of the agro-steppe system, cereal growing and livestock growing, affect Great Bustard demographic processes. Therefore, I explore whether trends in Great Bustards differ in relation to the relative landscape composition of sites in the study area, i.e. those dominated by arable agriculture or by pastoral systems.

Investigating trends in Great Bustard numbers in replicate subpopulations as independent observations increases statistical power, particularly as different subpopulations have experienced different rates and types of land-use and livestock change. This work aims to contribute to the knowledge of the effects of land-use and livestock changes on biodiversity, and to aid local land-managers to devise better conservation tools for agro-steppe birds in Iberia.

3.3 Methods

3.3.1 Study area and overview of agricultural system

This study focuses on the autonomous community of Extremadura in Spain, which is divided into two provinces – Cáceres in the north (19,868 km^2) and Badajoz in the south (21,766 km^2) – and on Alentejo province (31,551 km^2) in Portugal. Together, Extremadura and Alentejo form a contiguous region, with dimensions of roughly 350 km × 350 km (Fig. 1). The open landscapes that covered substantial parts of Extremadura and Alentejo were originally dominated by a traditional rotational system of arable cereal and fallow crops and low-intensity sheep grazing (Suárez, Naveso & De Juana 1997; Correal *et al.* 2003). In this agricultural system, cereals (mainly wheat and barley) are sown typically in June and July (Olea & Miguel-Ayanz 2006). After cereal harvest, livestock grazing typically spreads out from winter grazing grounds on fallows, pastures and other grasslands onto stubble as well (Correal *et al.* 2003). However, during late March and early April, when Great Bustards are counted (see below), livestock are normally concentrated on fallows, pastures and grasslands, and rarely cereals.

Intensification of agricultural systems has accelerated across the region since Spain and Portugal joined the EU in 1986, especially through the introduction of the Common Agricultural Policy (CAP) in 2003 (Brady *et al.* 2009). In extensive agricultural systems, CAP promoted increased agricultural productivity involving an increase in irrigated crops, decrease in fallows and stubbles, and increased livestock densities (Donald *et al.* 2002; Jones *et al.* 2011). For example, in Castro Verde in southern Alentejo, between 2000–2002 and 2008–2010, the area occupied by

cattle and sheep increased by 34% and 50% respectively, while the area of traditional grazing and annual crop systems decreased by 65% and 54% respectively (Ribeiro *et al.* 2014). In accordance with increased livestock numbers, the area used for hay production has also increased in the region (Faria, Morales & Rabaça 2016a). Agroforestry was noted as a cause for local extirpation and two local declines of Great Bustards in Portugal (Pinto *et al.* 2005). Agroforestry has also developed in the region, e.g. in the Mértola district (Alentejo) the area dedicated to agroforestry rose from 1% in 1986 to 22% in 2006 (Jones *et al.* 2011).

3.3.2 Great Bustard counts

Counts of Great Bustards during the lekking season (late March – early April) have been carried out in Extremadura by Junta de Extremadura and by Joachim Hellmich on behalf of WWF Spain, and in Alentejo by Instituto da Conservação da Natureza e das Florestas (ICNF). In Alentejo, counts have been almost annual (31 between 1980 and 2014). In Extremadura 12 annual counts took place in Cáceres between 1981 and 2014, and in Badajoz nine counts took place during that period. Despite slight variations in methodology and frequency of counts between different data sources, data are comprehensive and comparable across space and time. Details of the methodology used to count Great Bustards by the different sources, and about possible caveats and biases in the count data and how these were dealt with, are elaborated in Chapter 2.

3.3.3 Definition of subpopulations and measurement of temporal trends

An appropriate spatial scale is needed in order to seek to relate local responses of Great Bustards to land-use changes. The semi-independent demographic unit of 'subpopulation' was used, based on adult male locations in spring during the breeding season. At this time, males loosely aggregate and display in traditional lekking areas, typically covering several tens of square kilometres, into which females move to mate; depending on the distance between such areas, these gatherings are defined as subpopulations, with 16 in the study area (Fig. 3.1; full details about the methodology used to define subpopulations, and the limitations of this method, are elaborated in Chapter 2). During the breeding season local movements of adults and young birds occur regularly within subpopulations, but movements between subpopulations are considered to be rare and irregular. Therefore, changes of Great Bustard numbers in subpopulations are assumed to result from internal changes in rates of mortality, reproduction and recruitment, and to be influenced by land-use changes in that locality.

Figure 3.1: Extremadura (Spain) and Alentejo (Portugal) provincial borders (black lines) and their location in southwestern Iberia (see inset), Great Bustard subpopulations (grey polygons, named) and municipal boundaries in Extremadura and Alentejo (thin grey lines).

Because of relatively few counts in Extremadura, some subpopulations did not have counts in those years for which land-use data were available or for the start and end point of the periods analysed for population change. Therefore, LOESS models fitted to annual subpopulation counts between 1985 and 2014 were used to predict subpopulation numbers in missing years (see Chapter 2 for full

methodology of this procedure). The subpopulation of Montijo had too few data points to generate a reliable LOESS model and calculate trends, and was excluded from the analyses.

To calculate subpopulation trends over intervals between years when land-use data are available, following basic concepts in e.g. Southwood *et al.* (1974) and Krebs (2001), mean annual geometric population growth rates (λ) were used over each discrete period, calculated as $\lambda = e^{[(Ln(Nt+1)) - (Ln(No+1))] / t}$ where N_o is the number of Great Bustards at start year (e.g. 2006), N_t is the number of Great Bustards at end year (e.g. 2012), and t is the number of years between start year and end year.

3.3.4 Land-use and infrastructure data

For this study two open-access agricultural data sources that provide information on land-use were used. CORINE Land Cover (hereafter CLC, downloaded from http://www.eea.europa.eu/publications/COR0-landcover) is used to detect land-use changes, and data from Agrarian Surveys (hereafter AS, downloaded from www.ine.es [Extremadura] and www.ine.pt [Alentejo]) are used to detect livestock density changes. CLC and AS data are available for different years, so they cover different time periods in different intervals. Therefore, Great Bustard responses to land-use changes and to livestock density changes are analysed separately.

CLC is a pan-European land cover open-access mapping project, carried out by the European Environment Agency, and provides four detailed profiles of land use for four of the past 22 years – 1990, 2000, 2006 and 2012. For each snapshot in time, a satellite-derived layer of coarse land-cover types is available that allows calculation of the area of each land-use type in any defined region with a minimal cartographic unit of 25 ha (European Environment Agency 2007). CLC advantages include the complete and consistent geographic coverage of the entire study area and spatially explicit structure of the data that allows detection of land-cover type changes within defined subpopulations.

CLC land-cover types were aggregated into land-use classes relevant to Great Bustards at two levels of resolution. First, I considered models that related subpopulation trends to detailed land-use classes that included non-irrigated arable land, pastures and grasslands, agricultural non-habitat and non-agricultural non-habitat. Second, I examined models that aggregated favourable land-uses (pooled

as ‘habitat’) and unfavourable land-uses (pooled as ‘non-habitat’) (a list of these land-cover classes and their corresponding CLC land-cover categories is in Table 3.1).

Table 3.1: Explanation of land-use classes used as predictors in analyses, based on CLC aggregated land-cover types, downloaded from https://www.eea.europa.eu/publications/COR0-part2.

Detailed land-use classes and definition of contributing CLC land-cover types	***Aggregated land-use classes***
Non-irrigated arable land (CLC code 211)*: Lands under a rotation system used for annually harvested plants and fallow lands, which are not irrigated. These crops include cereals, dry legumes, fallow land, fodder crops and dry fields. Components of the rotation system.*	***Habitat****:* *Sum of non-irrigated arable land, permanent pastures and grasslands.*
Pastures and grasslands*:* *Permanent pastures (CLC code 231) are lands, which are permanently used (at least 5 years) for fodder production. Includes natural or sown herbaceous species, unimproved or lightly improved meadows and grazed or mechanically harvested meadows (i.e. hay). 'Natural' Grasslands (CLC code 321) are areas with herbaceous vegetation (maximum height is 150 cm and gramineous species are prevailing) which cover at least 50% of the surface covered by vegetation which developed under a minimum human interference (not mowed, fertilized or stimulated by chemicals which might influence production of biomass).*	
Agricultural non-habitat*: Permanent and irrigated crops. Including permanently irrigated land (CLC code 212), olives (CLC code 223), vineyards (CLC code 221), agroforestry (CLC code 244), and annual crops associated with permanent crops (typically cereals grown in Cork Oak plantations, CLC code 241).*	***Non habitat****:* *Sum of agricultural and non-agricultural non-habitat.*
Non-agricultural non-habitat*: Anthropogenic land-uses, planted forests and wetlands, including urban and suburban land-cover types, water bodies, mixed cultivation with housing, construction sites, mineral extraction, roads, railway lines, airports, planted coniferous and mixed forests.*	

Changes in the extent of land-use classes were calculated as proportionate change, defined as the absolute change in area of land-use class relative to subpopulation area: ('Habitat'$_{t+1}$– 'Habitat'$_{t}$) / (subpopulation area).

CLC may have some limitations in identification of land-use classes, based on the spatial resolution of maps it is projected on. In a modelling study testing the

effectiveness of CLC in identification of CLC classes in NW Spain, CLC was found to have limitations in classification of land-use classes at increasing spatial resolutions of maps (García-Llamas *et al.* 2016). In order to verify the use of CLC to track temporal changes in land-cover types favoured by Great Bustards, a field validation of CLC was carried out. In April and May 2017, habitat within 445 locations each of 125 m radius, distributed in eight subpopulations across Extremadura (n=227) and Alentejo (n=218) was recorded. Locations of these circles were pre-selected in the most recent CLC available, from 2012, either in non-irrigated arable land (n=204) or in pastures and grasslands that cannot be separated in the field (n=241), but not in other land-cover types. Habitat in each circle was characterised by a dominance index, in which each circle was visually divided into 8 equal sections; then for each habitat type, the number of sections in which it is dominant was recorded. Only circles with a score of 8 homogeneous habitat sections were selected for this validation. For each circle, land-cover type in CLC 2012 was compared with in-situ habitat recorded in 2017. There was a good match between CLC 2012 land-cover type and in-situ habitat: in 96% of non-irrigated arable land circles, and 97% of pastures and grasslands circles.

AS provide municipal numbers of cattle, sheep and goats, and land-use statistics as well (see explanation below). Because of the municipal structure of the data, it is unclear whether livestock and the potential available land for grazing are evenly distributed within each municipality. I assume that the municipal figures reflect the situation where Great Bustards are concentrated within municipalities. Therefore, the structure of the data allows only estimation of livestock densities and land-uses within subpopulation boundaries. Municipalities in Alentejo are

fewer and larger (n=62, mean=62.6 km^2, SD=38.5 km^2) than in Extremadura (n=392, mean=11.6 km^2, SD=16.5 km^2; see Fig. 1). As a result, in Alentejo the mean proportion of municipalities that overlap with subpopulations (n=36 municipalities, mean=0.39, SD=0.35) was lower than in Extremadura (n=220, mean=0.52, SD=0.37). Therefore, livestock data from Alentejo are coarser and potentially contain larger errors.

In Extremadura, AS data are available online for 1999 and 2009 providing only one interval of change (1999–2009); in Alentejo, AS data are available online also for 1989, providing two intervals of change (1989–1999, 1999–2009). Two subpopulations that stretch across borders, Northern Alentejo–Western Badajoz, and Mourão–Villanueva del Fresno, were included in analyses only in years when AS data were available from both sides of the border (1999 and 2009).

A strong advantage of AS data is that municipal statistics on the extent of detailed land-use types are available too for the same years – 1989 (Portugal only), 1999 and 2009. AS land-use data, both in Spain and Portugal, provide the municipal area of detailed categories of land-uses. In this study, land-uses relevant to Great Bustards were regarded separately: temporary pastures (apparently including pastures and fallows, but no detailed description for AS land-use data is available) and permanent pastures, cereals for grain, dry legumes for grain (i.e. chickpeas), and fodder crops. These land-use data allow calculation of municipal livestock densities, by dividing the livestock numbers by the area of pastures (and fallows that are assumed to be available for grazing), as this is where livestock are

concentrated during the period in which Great Bustards are counted, in late March and early April (Correal *et al.* 2003; Alonso *et al.* 2005a).

Hay is an increasing component of the agro-pastoral system in the study area (Faria, Morales & Rabaça 2016a). Both in CLC and AS it is treated with some uncertainty. In CLC, fodder crops are not represented by a unique land-cover type, but may be included both in non-irrigated arable land and in pastures. In AS, a unique category of fodder crops is defined, but it is unclear whether these fodder crops include only hay or also other fodder crops like legumes. Due to this uncertainty, it was impossible to include hay as a predictor in the analyses.

To test whether AS land-use data are related to equivalent CLC data, I performed a regression of AS 2009 municipal area of permanent pastures (dependent) related to CLC 2012 municipal extent of pastures and grasslands per municipality (predictor), across Extremadura and Alentejo (n=454 municipalities). Results showed a strong correlation between the two land-use data sources ($r=0.91$, $SE=0.001$, $p<0.0001$), although it produced a slope of 0.75, meaning that AS underestimate the combined area of grassland and pastures by 25% relative to CLC. As livestock are not on hay (a fodder crop) in spring, and AS measure of pastures excludes hay, livestock density calculated using AS data (in terms of livestock number per area of pasture) is relevant for spring livestock grazing density. Acknowledging the various potential biases and errors in AS and CLC data, AS livestock and land-use data and CLC land-use data are regarded as valid for my analyses.

For each subpopulation, mean livestock density weighted by relative area contribution of each municipality was calculated using the following equation: $S = \sum_i^n Pi * \varrho$, where *S* is the livestock density (number of livestock divided by area of AS pastures) of a subpopulation that overlaps with municipalities *i* to *n*, P_i is the proportion of the subpopulation area that overlaps with municipality *i*, and ϱ_i is the livestock density of the municipality. Changes in livestock densities used the same metric of annual geometric growth rate used to calculate subpopulation trends (λ, see above).

Subpopulation livestock density values were calculated separately for (1) cattle, (2) sheep and goats combined, and (3) total Livestock Units (LSU, whereas 1 LSU =1 cow or 10 goats and sheep, e.g. 2 cows and 10 sheep = 3 LSU).

3.3.5 Statistical analysis

Because CLC and AS data are only available for four and three years respectively with different interval lengths between data years, models related changes in Great Bustard numbers in subpopulation per interval to changes in land-use over the same interval, with subpopulation-period as the unit of replication.

The modelling processes were based on model inference, where complex models were compared to simple or null models based on changes in AICc values (second-order bias correction Akaike information criterion, Burnham & Anderson (2004)), to select the most parsimonious models with strongest support. A decrease of 2 AICc units or more indicates strong support, following Burnham & Anderson (2004). Models that were within 2 AICc units from null models were not supported.

A generalised linear model (GLM) that related subpopulation-period-specific λ (unit of replication; n=43 trends) to subpopulation ID (n=15 subpopulations, factorial) was not supported relative to the null model (ΔAICc=14.46), thus subpopulation trends were not consistently different from each other (across time periods). Additionally, a GLM that related subpopulation-period-specific λ to period (n=3, factorial) was not supported relative to the null model (ΔAICc=6.26), thus trends were not consistently different between CLC periods (across replicate subpopulations) (Table 3.2). Therefore, subpopulation identity and period were excluded from subsequent models that related period-specific subpopulation λ to changes in land-use.

Table 3.2: Results of General Linear Models relating Great Bustard period-specific subpopulation λ (43 trends across 15 subpopulations and three time periods) to subpopulation identity, to time period and to both. ΔAICc values are changes in AICc compared to the model with the lowest AICc value. **Bold** means support for this model.

Model	***B(SE)***	***AICc***	***ΔAICc***
Null		***-45.37***	***0***
Period	*-0.004(0.026)*	*-43.06*	*2.31*
Subpopulation identity		*-30.91*	*14.46*
Period *Subpopulation identity*	*-0.025(0.022)*	*-27.26*	*18.11*

In order to test the prediction that subpopulations dominated by pastoral agriculture showed different trends from subpopulations dominated by arable agriculture, a GLM that related period-specific subpopulation λ to the ratio between the proportionate area of CLC pastures and grasslands, and non-irrigated arable land (n=43 trends), was compared with a null model. Square-rooted-arcsine transformations of the proportions were used.

In order to test the prediction that there was a link between subpopulation λ and changes in the extent of CLC-based land-use classes, GLMs that related subpopulation λ to change in the extent of detailed and aggregated land-use classes in subpopulations (n=42 trends) were used separately.

In order to test the prediction that subpopulation λ might show a lagged response to changes in the extent of CLC-based land-use classes, these analyses were repeated with subpopulation λ calculated with six-year lags after CLC years (n=28 trends). The number of subpopulation-period-specific trends used in this

analysis is lower because six-year-lag after 2012 did not allow the calculation of trends for this future period.

In order to test the prediction that subpopulation λ were linked to livestock densities, GLMs that related subpopulation λ to livestock density changes in that subpopulation were compared to the null model and used separately for cattle, sheep and goats, and LSU, because of the small sample size (n=18 subpopulation-period-specific λ). Results of these GLMS were then used to predict subpopulation trend outcomes in different livestock density changes.

All analyses were carried out in RStudio version 2.15.0 (R Core Team 2017), using package MuMIn (Bartoń 2013) to obtain AICc values.

3.4 Results

3.4.1 Overview of demographic processes in Great Bustard subpopulations

There was non-significant variation in period-specific subpopulation λ (n= 43, 15 subpopulations, three time periods) between subpopulations and between CLC periods: no support was found for GLMs relating λ to subpopulation identity (factorial) or to CLC period compared to null model (Table 3.2). Out of 15 subpopulations, 11 showed consistent λ across the three time periods (either consistently decreasing or consistently increasing), while four subpopulations switched trend directions between periods (Table 3.3). Between 1990 and 2000, mean λ was 0.981 (SD=0.073, CI95%= 0.943–1.019, n=14 subpopulations). Between 2000 and 2006, mean λ was 1.048 (SD=0.205, CI95%= 0.940–1.156, n=14). Between 2006 and 2012, mean λ was 0.987 (SD=0.098, CI95%, 0.936–1.038, n=14). Based on confidence intervals, mean λ of each time period was not significantly different from 1.

Table 3.3: Period-specific annual geometric growth rates for each of 15 Great Bustard subpopulations included in trends analyses (Tables 6 and 7) during three time periods: 1990 to 2000, 2000 to 2006, 2006 to 2012. Mean rates, SD and 95% CI's are also shown for each time period. Missing values indicate the subpopulation did not contain any Great Bustards during that time period.

Subpopulation	***1990 to 2000***	***2000 to 2006***	***2006 to 2012***
La Mata	*1.011*	*1.124*	*1.001*
Guijo de Coria	*0.957*	*0.957*	*0.901*
Central Caceres	*0.999*	*0.996*	*0.990*
San Vicente de Alcantara	*0.941*	*0.890*	*0.975*
Campo Lugar	*0.978*	*0.929*	*1.182*
La Serena	*1.082*	*1.034*	*0.894*
Retamal	*1.032*	*1.045*	*1.012*
Campina Sur	*0.999*	*0.952*	*0.972*
Villanueva del Fresno - Mourao - Safara	*0.971*	*0.831*	*0.825*
Northern Alentejo and western Badajoz	*0.983*	*1.028*	*0.929*
Evora	*0.963*	*0.939*	*0.940*
Cuba	*1.024*	*1.191*	*1.174*
Moreanes		*1.682*	*0.987*
Castro Verde	*1.029*	*1.074*	*1.036*
Castelo Branco	*0.763*		
Mean	*0.981*	*1.048*	*0.987*
SD	*0.073*	*0.205*	*0.098*
95% upper CI	*1.019*	*1.156*	*1.038*
95% lower CI	*0.943*	*0.940*	*0.936*

3.4.2 Overview of agricultural changes across Extremadura and Alentejo

Based on CLC data, the total area of non-irrigated arable land (pooled across all 16 subpopulations) decreased by 42.8% between 1990 and 2012, the area of pastures and grasslands increased by 5.5%, the area of agricultural non-habitat increased by 20%, and the area of non-agricultural non-habitat decreased by 20% (Fig. 3.2). However, there was considerable variation in land-use changes among subpopulations that experienced different rates of land-use change. Across individual subpopulations, the mean change in non-irrigated arable land was a decrease of 29.7% but with high variability (SD=27.4%) and wide 95% confidence intervals of 45%, while for pastures and grasslands it involved an increase of 28.3% (SD=91.2%) and wide 95% confidence intervals of 45%. Agricultural non-habitat increased by a mean of 38.3% (SD=53.2%). Non-agricultural non-habitat decreased by a mean of 11% (SD=34.5%).

When these land-use classes were aggregated to 'habitat' and 'non-habitat', the total area of habitat suitable for Great Bustards (pooled across all subpopulations) decreased by 32% between 1990 and 2012, and the area of unsuitable habitat increased by 6% (Fig. 3.2). Again, there was considerable variation across individual subpopulations, with habitat decreasing by a mean of 23.8% (SD=35.4%), and non-habitat increasing by a mean of 10.7% (SD=37.2, Fig. 3.3).

There were significant mean increases in cattle densities in subpopulations in Alentejo between 1989 and 1999 (mean=1.027, CI 1.015–1.039), in goats and sheep densities in all subpopulations between 1999 and 2009 (mean=1.064, CI

1.026–1.103), and in LSU densities in Alentejo between 1989 and 1999 (mean=1.025, CI 1.010–1.040) (Table 3.4). There was a marked increase between 1999 (1989 in Alentejo) and 2009 in densities of cattle in three of the 16 subpopulations, in 12 subpopulations sheep and goat density increased, and in six subpopulations LSU density increased (Figs. 3.4a-c). Changes in LSU density were primarily affected by changes in cattle density (regression of LSU density changes in response to changes in cattle density: R^2=0.69, $F_{1,16}$=36.69, p<0.0001; in response to changes in sheep and goat density: R^2=0.16, $F_{1,16}$=4.31, p=0.054). No correlation was found between changes in cattle densities and changes in sheep and goat densities (r=-0.016, SE=0.908, p=0.95). In 1999 and 2009, the overall contribution of cattle numbers to LSU across all municipalities was 90.97% and 63.32% respectively.

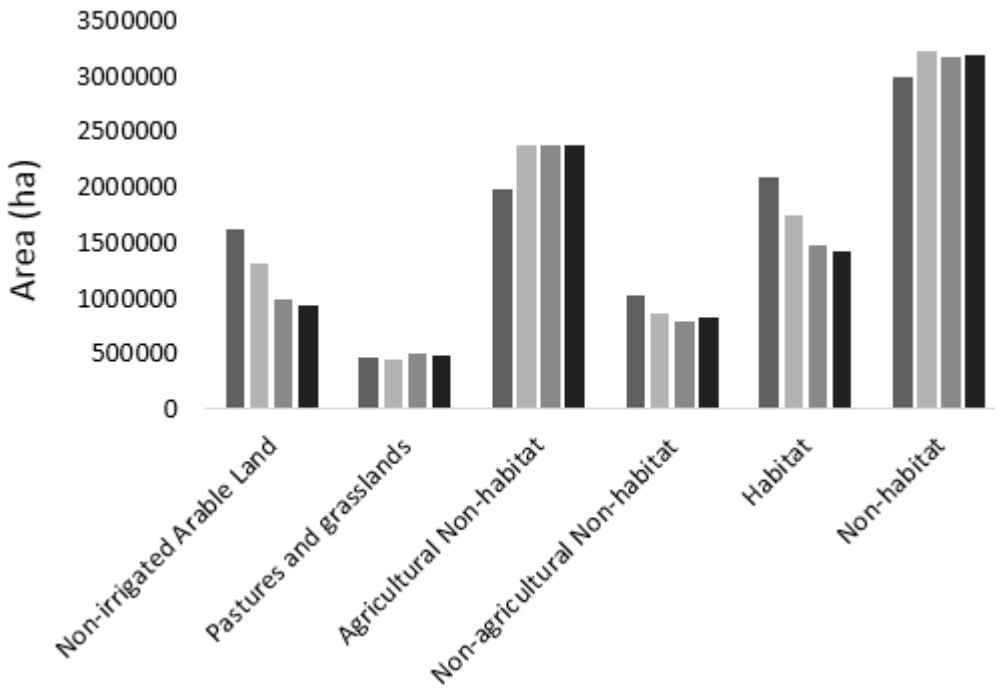


Figure 3.2: Overall temporal changes in area of land-use classes in subpopulations across the study area in Extremadura and Alentejo, 1990 – 2012. ■ are data from 1990. ■ are data from 2000. ■ are data from 2006. ■ are data from 2012.

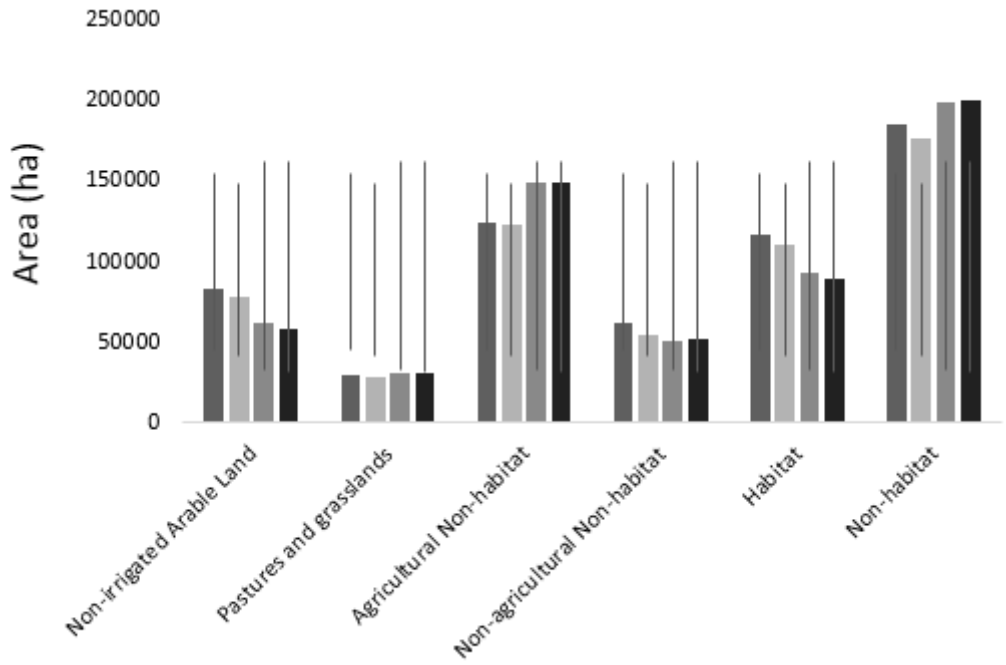
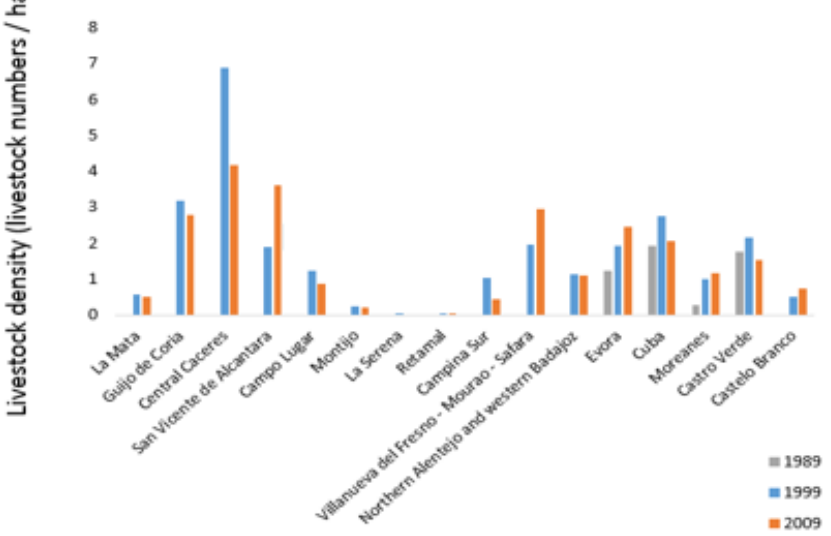


Figure 3.3: Mean temporal changes in area of land-use classes in 16 subpopulations in Extremadura and Alentejo, 1990 – 2012. ■ are data from 1990. ■ are data from 2000. ■ are data from 2006. ■ are data from 2012. Vertical thin lines are standard deviations.

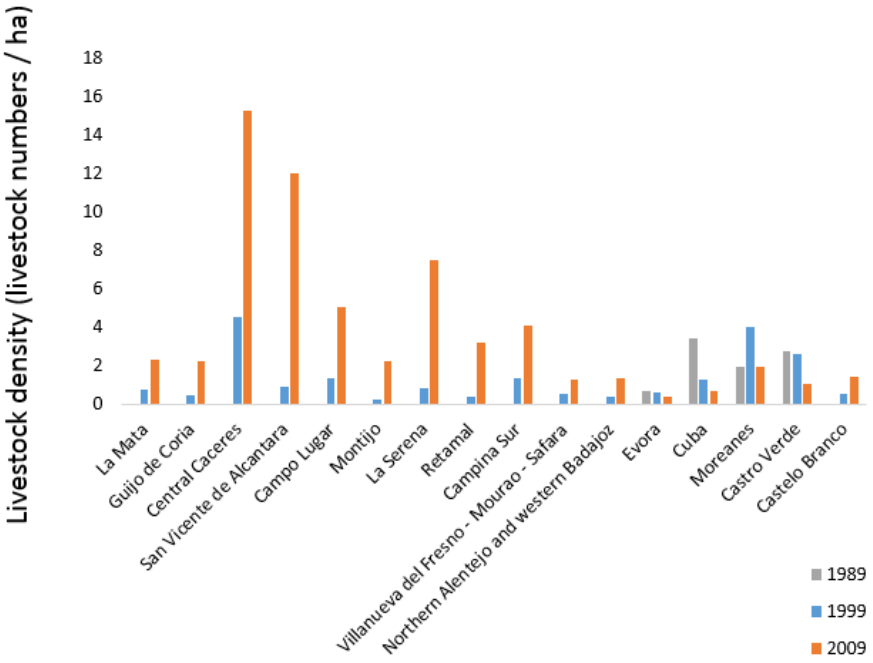
Table 3.4: Changes in livestock densities in subpopulations (n=16) in Extremadura and Alentejo, including Montijo (which was excluded from trends analyses) (Tables 6 and 7). Between 1989 and 1999, data are available only for Alentejo (n=4). **Bold** are mean changes significantly different from 1.

	Cattle		***Sheep***		***LSU***	
Subpopulation	***1989-1999***	***1999-2009***	***1989 - 1999***	***1999-2009***	***1989 - 1999***	***1999-2009***
La Mata		*0.995*		*1.065*		*1.005*
Guijo de Coria		*0.991*		*1.082*		*0.995*
Central Caceres		*0.959*		*1.113*		*0.979*
San Vicente de Alcantara		*1.047*		*1.211*		*1.068*
Campo Lugar		*0.983*		*1.100*		*1.001*
Montijo		*0.998*		*1.095*		*1.013*
La Serena		*0.999*		*1.163*		*1.047*
Retamal		*1.002*		*1.118*		*1.025*
Campina Sur		*0.967*		*1.079*		*0.985*
Villanueva del Fresno - Mourao - Safara		*1.029*		*1.038*		*1.030*
Northern Alentejo and western Badajoz		*0.998*		*1.052*		*1.002*
Evora	*1.027*	*1.017*	*0.995*	*0.985*	*1.026*	*1.016*
Cuba	*1.025*	*0.980*	*0.937*	*0.969*	*1.017*	*0.978*
Moreanes		*1.008*		*0.949*		*0.998*
Castro Verde	*1.013*	*0.978*	*0.996*	*0.947*	*1.011*	*0.974*
Castelo Branco	*1.043*		*1.045*		*1.046*	
Mean	***1.027***	*0.997*	*0.993*	***1.064***	***1.025***	*1.008*
SD	*0.012*	*0.023*	*0.044*	*0.077*	*0.015*	*0.026*
95% upper CI	*1.039*	*1.008*	*1.036*	*1.103*	*1.040*	*1.021*
95% lower CI	*1.015*	*0.985*	*0.950*	*1.026*	*1.010*	*0.994*

A: Cattle



B: Sheep and goats



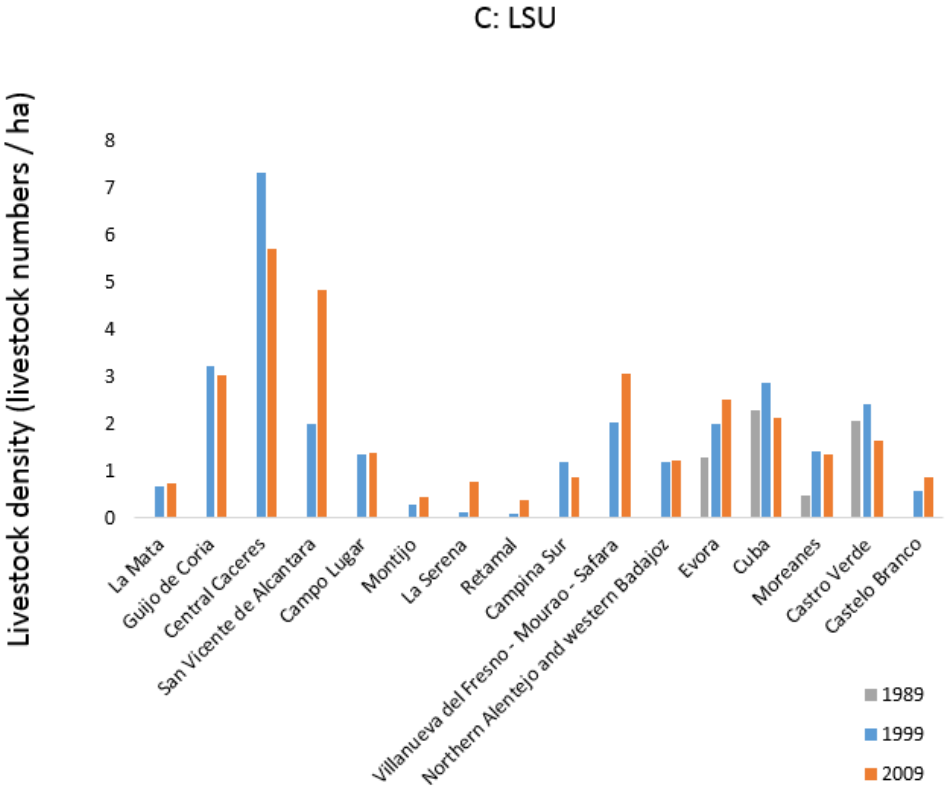


Figure 3.4: Changes in (A) cattle densities (B) sheep and goat densities (C) LSU in Great Bustard subpopulations in Extremadura and Alentejo between 1989 and 2009.

Cattle numbers (AS, square-rooted) were positively correlated with the area of permanent pastures (AS, square-rooted): (454 municipalities in Extremadura and Alentejo: $r=0.743$, $p<0.0001$). AS cattle numbers were also positively correlated with AS area of hay (fodder crops) ($r= 0.753$, $P<0.0001$).

3.4.3 Great Bustard subpopulation trends related to land-use changes

Great Bustard subpopulation trends were more positive in subpopulations where arable agriculture was more dominant based on the negative slope of the relation between subpopulations trends and the ratio between the proportionate area of pastoral land-uses and arable land-uses (B=-0.038, Table 3.5), although the difference in trends between subpopulations dominated by arable agriculture and subpopulations dominated by pastoral agriculture was not significant. The relation between subpopulation trends with the ratio of the proportionate area of pastures and grasslands (out of the entire subpopulation area), and the proportionate area of non-irrigated arable land (n=43 subpopulation trends), did not receive strong support relative to an intercept-only null model (ΔAICc=0.06, Table 3.5).

Table 3.5: Results of general linear models relating period-specific λ in Great Bustard subpopulations to the ratio between the arcsine-square root-transformed proportionate area of pastures and grasslands out of the entire subpopulation area and the arcsine-square root-transformed proportionate area of non-irrigated arable land out of the entire subpopulation area (43 trends in 15 subpopulations across three time-periods). ΔAICc values are changes in AICc compared to the model with the lowest AICc value. **Bold** means support for this model.

Model	***B(SE)***	***AICc***	***ΔAICc***
Null		***-45.37***	***0***
Ratio	*-0.038(0.026)*	*-45.38*	*-0.01*

Relating period-specific subpopulation λ to changes in the extent of detailed land-use classes, no support was found for models that included changes in the extent of non-irrigated arable land (ΔAICc=1.07), pastures and grasslands (ΔAICc=4.09), agricultural non-habitat (ΔAICc=2.02) and non-agricultural non-habitat (ΔAICc=0.66) relative to the intercept-only null model (Table 3.6a; parameter CIs overlap zero, Fig. 3.5a). Similarly, in models relating period-specific subpopulation λ to changes in the extent of aggregated land-use classes, no support was found for the effect of habitat (ΔAICc=0.87), or non-habitat (ΔAICc=0.65) (Table 3.6b; parameters CIs overlap zero, Fig. 3.5b).

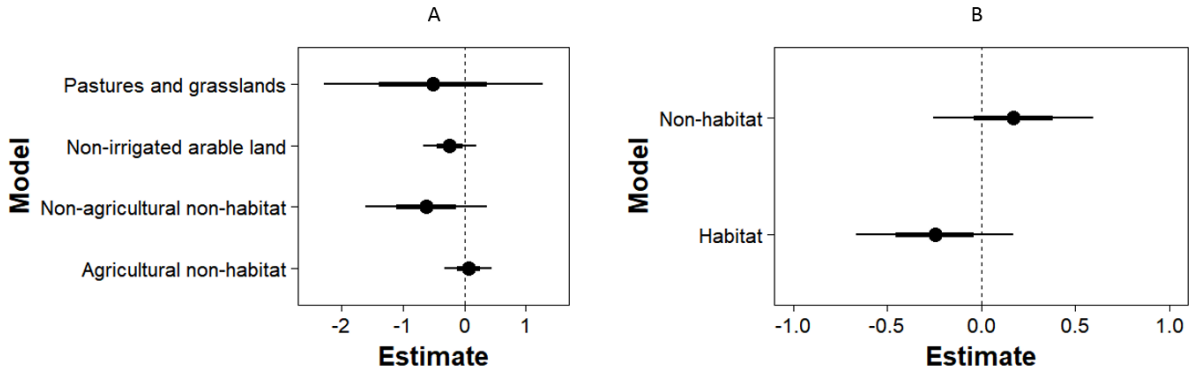


Figure 3.5A and 3.5B: effect sizes (circles), standard errors (thick lines) and 95% confidence intervals (thin lines) of models relating subpopulation trends to changes in extent of CLC-based detailed land-use classes (A) and aggregated land-use classes (B).

Table 3.6a: Results of general linear models relating subpopulation-period-specific λ in 15 Great Bustard subpopulations, over three discrete time periods (n=43 trends) to changes in extent of four detailed land-use classes. Models are ranked according to increasing AICc values. For each model, B(SE) of each predictor used are shown; model without any parameters shown is the null model. Models with * indicate alternative null models that include subpopulation (categorical) or period. ΔAICc values are changes in AICc compared to the model with the lowest AICc value. **Bold** represents strong support for the model.

Agricultural non-habitat	*Non-agricultural non-habitat*	*Non-irrigated arable land*	*Pastures & grasslands*	*Subpop'n*	*Period*	*df*	*AICc*	*ΔAICc*
						2	***-45.37***	***0***
	-0.619(0.486)					*3*	*-44.71*	*0.66*
	-0.759(0.490)	*-0.304(0.216)*				*4*	*-44.35*	*1.02*
		-0.237(0.215)				*3*	*-44.30*	*1.07*
0.067(0.190)						*3*	*-43.17*	*2.20*
					*	*2*	*-43.06*	*2.31*
0.052(0.189)	*-0.610(0.493)*					*4*	*-42.34*	*3.03*
0.065(0.189)		*-0.236(0.217)*				*4*	*-41.98*	*3.39*
0.046(0.187)	*-0.751(0.498)*	*-0.302(0.218)*				*5*	*-41.83*	*3.54*
			-0.504(0.876)			*3*	*-41.28*	*4.09*
	-0.766(0.533)		*-0.847(0.900)*			*4*	*-40.98*	*4.39*
	-0.914(0.535)	*-0.319(0.219)*	*-0.931(0.885)*			*5*	*-40.67*	*4.70*
		-0.248(0.220)	*-0.517(0.873)*			*4*	*-40.16*	*5.21*
0.075(0.194)			*-0.528(0.888)*			*4*	*-38.97*	*6.40*
0.061(0.192)	*-0.757(0.540)*		*-0.863(0.909)*			*5*	*-38.49*	*6.88*
0.057(0.189)	*-0.905(0.543)*	*0.318(0.222)*	*-0.945(0.898)*			*2*	*-38.01*	*7.36*
0.073(0.193)		*-0.248(0.223)*	*-0.541(0.885)*			*5*	*-37.72*	*7.65*
				*		*2*	*-30.91*	*14.46*

Table 3.6b: Results of general linear models relating λ in Great Bustard subpopulations to proportionate changes in extent of two aggregated land-use classes (15 subpopulations, 42 changes, over three discrete time periods). Models are ranked according to increasing AICc values. For each model, B(SE) of each predictor used are shown. Model without B(SE) is null model. ΔAICc values are changes in AICc compared to the model with the lowest AICc value. **Bold** represents strong support for the model.

Habitat	***Non-habitat***	***df***	***AICc***	***ΔAICc***
		2	***-45.37***	***0***
	0.171(0.211)	*3*	*-44.72*	*0.65*
-0.246(0.207)		*3*	*-44.50*	*0.87*
-0.243(0.208)	*0.166(0.210)*	*4*	*-42.72*	*2.65*

When these analyses were repeated with six-year-lagged subpopulation λ, no support was found for models that included changes in the extent of non-irrigated arable land (ΔAICc=1.50), pastures and grasslands (ΔAICc=2.15), agricultural non-habitat (ΔAICc=2.13) and non-agricultural non-habitat (ΔAICc=1.71) relative to the intercept-only null model (Table 3.7a). Examining the link between six-year-lagged subpopulation λ and changes in the extent of aggregated land-use classes, no support was found for models that included habitat (ΔAICc=0.29), and non-habitat (ΔAICc=2.52) (Table 3.7b).

Table 3.7a: Results of general linear models relating six-year-lagged λ in Great Bustard subpopulations to changes in extent of four detailed land-use classes (15 subpopulations, 28 changes, over two discrete time periods). Models are ranked according to increasing AICc values. For each model, B(SE) of each predictor used are shown; model without any parameters shown is null model. ΔAICc values are changes in AICc compared to the model with the lowest AICc value. **Bold** represents strong support for the model.

Agricultural non-habitat	*Non-agricultural non-habitat*	*Non-irrigated arable land*	*Pastures and grasslands*	*df*	*AICc*	*ΔAICc*
				2	***-48.64***	***0***
		-0.224(0.156)		*3*	*-48.27*	*0.37*
			-0.339(0.661)	*3*	*-46.41*	*2.23*
-0.031(0.143)				*3*	*-46.18*	*2.46*
	-0.069(0.382)			*3*	*-46.16*	*2.48*
	-0.240(0.388)	*-0.254(0.165)*		*4*	*-45.96*	*2.68*
		-0.228(0.158)	*-0.380(0.648)*	*4*	*-45.92*	*2.72*
-0.021(0.141)		*-0.223(0.159)*		*4*	*-45.56*	*3.08*
	-0.124(0.399)		*-0.392(0.694)*	*4*	*-43.78*	*4.86*
-0.027(0.146)			*-0.331(0.675)*	*4*	*-43.71*	*4.93*
	-0.326(0.407)	*-0.270(0.167)*	*-0.527(0.678)*	*5*	*-43.67*	*4.97*
-0.032(0.146)	*-0.069(0.389)*			*4*	*-43.47*	*5.17*
-0.020(0.143)	*-0.240(0.396)*	*-0.252(0.168)*		*5*	*-43.00*	*5.64*
-0.016(0.143)		*-0.227(0.161)*	*-0.374(0.663)*	*5*	*-42.94*	*5.70*
-0.027(0.148)	*-0.124(0.407)*		*-0.385(0.709)*	*5*	*-40.83*	*7.81*
-0.012(0.144)	*-0.325(0.415)*	*-0.269(0.171)*	*-0.523(0.694)*	*6*	*-40.41*	*8.23*

Table 3.7b: Results of general linear models relating six-year-lagged λ in Great Bustard subpopulations to changes in extent of two aggregated land-use classes (15 subpopulations, 28 changes, over two discrete time periods). Models are ranked according to increasing AICc values. For each model, B(SE) of each predictor used are shown. Model without B(SE) is null model. ΔAICc values are changes in AICc compared to the model with the lowest AICc value. **Bold** represents strong support for the model.

Habitat	***Non-habitat***	***df***	***AICc***	***ΔAICc***
		2	***-48.64***	***0***
-0.222(0.151)		*3*	*-48.35*	*0.29*
	0.010(0.166)	*3*	*-46.13*	*2.51*
-0.223(0.154)	*0.020(0.163)*	*4*	*-45.63*	*3.01*

3.4.4 Links between Great Bustard subpopulation trends and changes in livestock densities

There was strong support for the model relating subpopulation trends to overall LSU density changes (ΔAICc=-2.4 compared to null model, 95% CI does not overlap zero), but not for models that included sheep and goat density changes (ΔAICc=-0.63) or cattle density changes (ΔAICc=0.06) individually. The explanatory power of the models was relatively poor (Fig. 3.6, Table 3.8). Subpopulation trends were negatively correlated with all livestock types (effect sizes, standard errors and confidence intervals are in Fig. 3.7). Based on these results, an annual decline of 2.8% in numbers of Great Bustards in a subpopulation is predicted for an annual increase of 2.6% in LSU density in that subpopulation. To reach stability in GB annual trends, an annual decrease of 0.1% in LSU density is required.

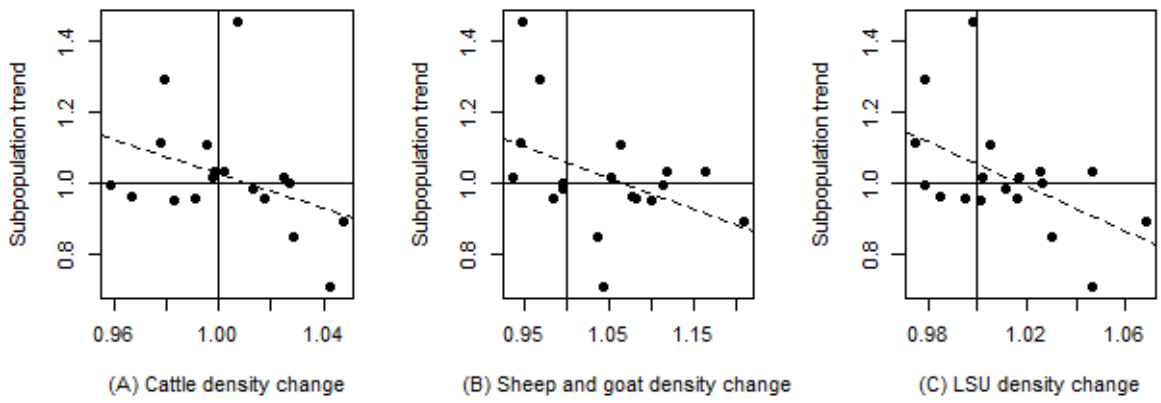


Figure 3.6: Trends of Great Bustard subpopulations in Extremadura and Alentejo related to changes in (A) cattle density (B) sheep and goat density (C) LSU density.

Table 3.8: Results of general linear models relating λ of Great Bustard subpopulations in Extremadura and Alentejo to changes in cattle, sheep and goats, and LSU densities in those subpopulations (15 subpopulations, 18 changes). ΔAICc values are changes in AICc values compared to the best supported model. **Bold** means strong support for this model. R^2 values are of General Linear Models using the same variables.

Model	***B(SE)***	***R^2***	***AICc***	***ΔAICc***
LSU	***-3.137(1.339)***	***0.256***	***-13.24***	***0***
Sheep and goats	*-0.879(0.472)*	*0.179*	*-11.47*	*1.77*
Null			*-10.84*	*2.40*
Cattle	*-2.463(1.486)*	*0.147*	*-10.78*	*2.46*

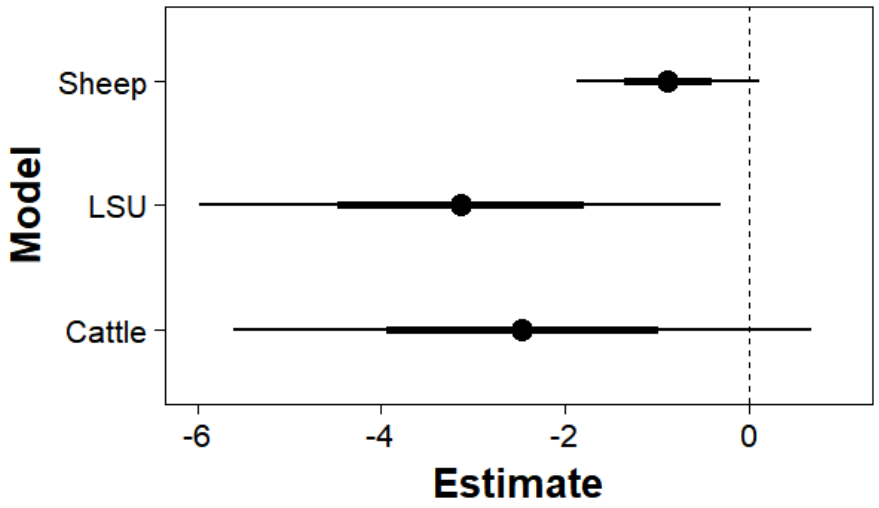


Figure 3.7: Effect sizes (circles), standard errors (thick lines) and 95% confidence intervals (thin lines) of models relating subpopulation trends to changes in livestock densities – sheep and goats, cattle, and LSU.

3.5 Discussion

Breeding Great Bustards select non-irrigated arable land, pastures and grasslands (e.g. Lane, Alonso & Martín 2001; Moreira, Morgado & Arthur 2004; Magaña *et al.* 2010; Rocha, Morales & Moreira 2012), and their subpopulations were therefore predicted to respond negatively to loss of such habitat and to the expansion of unfavourable habitats. However, no statistical link was found between period-specific Great Bustard subpopulation trends and changes in the extent of different land-use classes, both detailed and aggregated. For non-irrigated arable land, this result is surprising, as this land-use class is a major component of the traditional cereal–livestock grazing rotational system in Iberia (Correal *et al.* 2003; Caballero *et al.* 2009), and an important breeding habitat for Great Bustards in Iberia. This result may also be explained by misclassification of land-cover types by CLC, including mis-identification of direct-sown crops with the associated increases in pesticide use, and mis-identification of the loss of the traditional rotational agricultural systems to permanent cereal or livestock system (Ribeiro *et al*. 2014), or the abolition of compulsory fallows under 2008 CAP regulations (Matthews 2013), that prevented correct identification of land-use changes relevant to Great Bustards.

Other ecological forces than agricultural changes may be at play in this system. In the scenario of subpopulations in Extremadura and Alentejo that experienced moderate loss of breeding habitat, it is possible that Great Bustards may have the ability to relocate over short distances within subpopulations as a response to habitat loss, and concentrate in sections of subpopulations that maintain high-quality habitat. There is some indirect evidence to that - Pinto *et al.*

(2005) suggested through modelling that a concentration process over large distances has taken place in Castro Verde in southern Alentejo, as a result of processes of habitat improvement within and habitat loss outside the area. However, there is no tracking or ringing recovery evidence available yet demonstrating the capacity of Great Bustards to concentrate within subpopulations or migrate between subpopulations. It must be stressed that, in sites that undergo dramatic land-use changes, local extirpations may be expected, as reported in Pinto, Rocha, & Moreira (2005).

Despite not finding statistical support for models that incorporated lagged subpopulation trend responses to land-use changes, it is possible that the six-year lag period used in this study to detect demographic changes of Great Bustard in response to land-use changes is too short. CLC and GB data do not cover the years after 2012 and 2014 respectively, in which indications of declines in several Great Bustard subpopulations in Extremadura and Alentejo were reported (Chapter 2). It is possible that with extension of CLC data in the future, such a lagged demographic response to land-use changes can be detected.

The results suggest that, across the entire study area, changes in habitat quality may have a stronger effect on subpopulation trends than changes in habitat extent, based on the strong statistical support received by a model that linked Great Bustard subpopulation trends and LSU density changes. Although links between subpopulation trends and cattle densities or sheep and goat densities were not supported directly, the close visual relationship and similarity of effect sizes and directions (Fig. 3.7) found between cattle densities and LSU densities

imply that increases in cattle densities have contributed more to negative subpopulation trends. This is also supported by the lack of correlation found between changes in cattle densities and changes in sheep and goat densities. Despite the overall increase in the availability of pastures and grasslands across the study area (Fig. 3.2), livestock densities increased in some subpopulations (Fig. 3.4), which may lead to overgrazing, that may increase predation risk, and may reduce availability of at least some groups of arthropods that depend on taller grass, and/or higher levels of disturbance.

Importantly, the caveats in the data used for livestock density analyses should be brought into account when considering the different results. The tiny sample size (18 subpopulations changes), across two time periods only and with imbalanced numbers of changes per time period (two between 1989 and 1999, 16 between 1999 and 2009), and only two hypotheses testing links between subpopulation trends and livestock densities, indicate the need for caution in accepting the strong support received by the model linking subpopulation trends to LSU density changes. In an equivalent to Bonferroni correction, an increase of the strong support threshold in AICc values to 4 would result in no support at all.

With the increase in cattle numbers, hay production increased too. Hay fields might act as ecological traps (Gilroy *et al.* 2011; Hale & Swearer 2016) for breeding Great Bustards, as pastures are increasingly grazed by livestock, and females may be forced to breed in hay fields that are cut early and cause higher rates of nest mortality (Faria, Morales & Rabaça 2016a; b). Therefore, the pressure on Great Bustards breeding in the pastoral agricultural systems of Extremadura and

Alentejo is increasing. The results suggesting that Great Bustards respond negatively to increased livestock densities add to the understanding of the variation among species and spatial variation of bird responses to livestock grazing. This is also the first indication of long-term responses of birds to changes in livestock densities, at a landscape scale.

The mechanisms by which livestock grazing might affect Great Bustard subpopulation trends are not totally clear. Increased livestock densities could decrease breeding success in several ways. Nest destruction by trampling is a possible problem. In a small sample of Great Bustard nests studied in Alentejo, two out of 11 nest failures were as a result of sheep trampling (Rocha, Morales & Moreira 2012). Moreover, at high livestock densities, disturbance might increase to levels that reduce breeding success, by forcing females to breed in suboptimal microhabitats, or causing nest abandonment.

There are several more potential, indirect effects of increased livestock densities on breeding success of ground-nesting birds. It is possible that increased livestock grazing reduces nest safety against predators – female Great Bustards were found to select land-uses characterised by denser grass for breeding in central Spain, possibly for better concealment from predators (Magaña *et al.* 2010). Overgrazing might expose nests of females breeding in pastures and fallows to higher predations risks. It is also possible that increased livestock grazing reduces food availability for Great Bustard chicks, which are fed mainly on invertebrates (Gewalt 1959; Bravo *et al.* 2012). In different parts of the year, both Great Bustards and Little Bustards select land-uses that are rich in invertebrates (Lane *et al.* 1999;

Salamolard & Moreau 1999). In France, Little Bustard breeding productivity was positively related to grasshopper abundance (Bretagnolle *et al.* 2011). Livestock grazing was found to decrease grasshopper abundance (O'Neill *et al.* 2003, 2010), spider, bug and beetle numbers (Dennis *et al.* 2008) and Hymenoptera richness and diversity (Debano 2006), all important components of Great Bustard diet (Lane *et al.* 1999; Rocha, Marques & Moreira 2005). Therefore, it is likely that the limited availability during the breeding season of some invertebrates that requite tall grass affects fledging success of Great Bustards too in cases of intensive livestock grazing.

It is possible that other mechanisms rather than agricultural land-use changes contributed to trends of Great Bustard subpopulations in this region, hence the relatively little variance the models explain. Other factors that were suggested to have links with changes in Great Bustard numbers are hunting, which was banned in Spain and Portugal in the 1980s but apparently continues illegally (Alonso, Palacín & Martín 2003; Alonso *et al.* 2005b; c), general human disturbance (Sastre *et al.* 2009; Burnside *et al.* 2014), and development of infrastructure: powerlines, fences, roads, railways, and wind turbines (Lane, Alonso & Martín 2001; Alonso *et al.* 2005c; Raab *et al.* 2010). Construction of powerlines and wind-turbines in Europe increases mortality rates through collisions (Haas *et al.* 2005). Powerlines may also cause behavioural avoidance and change spatial use and migration routes (Raab *et al.* 2010; Palacín *et al.* 2016). Large species such as Great Bustard are more vulnerable to powerline collisions, especially when these structures form prominent features in an open area (Drewitt & Langston 2008). Fence collisions also increase mortality rates of farmland birds (Patten *et al.* 2005; Wolfe *et al.* 2007; Vadász & Lóránt 2014). It is possible that these factors affected

subpopulation trends in the study system as well by increasing adult mortality rates, but were not studied here thoroughly. In April–May 2017, data on fence densities were collected in eight subpopulations across Extremadura and Alentejo, counting fence intersections along 682 500 m transects (Appendix 3.1). These data demonstrated the current variation between subpopulations in fence densities. Long-term data on infrastructure development across all subpopulations might offer an insight on further factors affecting subpopulations trends.

The agricultural databases that the analyses used have limitations that might affect the results. The relatively poor explanatory power of models, especially in the analyses that link trends of Great Bustard subpopulations to land-use changes, may lead to inaccurate interpretation of the results. Both CLC and AS agricultural databases have limitations in classification of different types of agricultural practices and of livestock, and have large time steps between years that are covered by surveys (especially AS data), intervals that may not match speed of biological processes of Great Bustards. Additionally, changes in agricultural regimes that have been documented in Alentejo, such as the loss of the rotational system and direct sowing year after year (Ribeiro *et al.* 2014), and early sowing and harvest (João Paulo Silva, pers. comm.), are not detected in CLS or AS. It is possible that, with more elaborate and precise agricultural databases, intricate demographic responses of Great Bustards could be better detected. However, despite the medium-sized sample sizes and data limitations, the negative effects of livestock densities are clearly shown. This does increase my confidence in the results.

For the future sustainability of Great Bustard populations in Extremadura and Alentejo, and possibly for other associated farmland birds in the region as well, careful planning of the development of agricultural practices in the region is crucial. Protection of a sufficient amount of breeding habitat is a key, but the management of the existing habitats for conservation is also important. More specifically, reduction of livestock densities in areas that hold Great Bustards is especially challenging in respect to the large spatial effects of the CAP in Europe (Donald *et al.* 2002; Ribeiro *et al.* 2014), and the possible subsequent effects of CAP on farmland birds. However, it is important that the regional administrations in Extremadura and Alentejo find successful measures to allow sustainable agriculture, perhaps via the respective networks of Special Protection Areas – Zonas de Especial Protección para las Aves (ZEPA) in Spain, and Zonas de Protecção Especial (ZPE) in Portugal. Conservation-based management of protected areas in the region has the potential to lead to beneficial processes for biodiversity, potentially through the implementation of agri-environmental schemes (Brady *et al.* 2009). The example of Castro Verde in southern Alentejo is noteworthy. Implementation of agri-environmental schemes that included protection regulations restricting irrigation, afforestation and perennial crops, and adjustment of harvest cycles to conservation needs (Santana *et al*. 2014), led to outstanding increases of Great Bustards (Pinto *et al*. 2005), and to higher richness and abundance of several agro-steppe breeding bird species (Santana *et al.* 2014). With leadership and creativity of conservation managers, such success stories can be replicated in other parts of the region.

Future research in this field should address the effects of fine-scale agricultural changes and infrastructure development on farmland birds, and about

the role of protected areas as safe havens for agro-steppe bird species. Using fine and accurate agricultural databases, rather than coarse databases such as CLC and AS, may lead to interesting ecological insights into the responses of birds to agricultural intensification.

3.6 Acknowledgments

Great Bustard count data for this study were kindly supplied by Angel Sánchez (Junta de Extremadura), Marcia V. Pinto and Pedro Rocha (ICNF) and Joachim Hellmich (on behalf of WWF Spain). I thank the many rangers and ornithologists who took part in Great Bustard counts over the years. Special thanks to Agustín Mogena and to Joaquín Dávalos for their assistance in data collation and interpretation.

3.7 References

Alonso, J.C. (2014) The great bustard: past, present and future of a globally threatened species. *Ornis Hungarica*, **22**, 1–13.

Alonso, J.C., Alonso, J.A., Martín, C.A., Palacín, C., Magaña, M. & Martín, B. (2005a) Los censos de avutardas: aspectos metodológicos. *La Avutarda Comun en la Peninsula Iberica: Poblacion Actual y Metodo de Censo* (eds J.C. Alonso, C. Palacín, & C.A. Martín), p. SEO/BirdLife, Madrid.

Alonso, J.C., Martín, E., Alonso, J.A. & Morales, M.B. (1998) Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. *Behavioral Ecology*, **9**, 243–252.

Alonso, J.C., Martín, C.A., Palacín, C., Martín, B. & Magaña, M. (2005b) The great bustard *Otis tarda* in Andalusia, southern Spain: Status, distribution and trends. *Ardeola*, **52**, 67–78.

Alonso, J.C., Palacín, C. & Martín, C.A. (2003) Status and recent trends of the great bustard (*Otis tarda*) population in the Iberian peninsula. *Biological Conservation*, **110**, 185–195.

Alonso, J.C., Palacin, C., Martin, C.A., Mouati, N., Arhzaf, Z.L. & Azizi, D. (2005c) The Great Bustard *Otis tarda* in Morocco: A re-evaluation of its status based on recent survey results. *Ardeola*, **52**, 79–90.

Bartoń, K. (2013) MuMIn: multi-model inference, R package version 1.9.13.

Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings. Biological sciences / The Royal Society*, **278**, 1894–902.

Berg, Å., Wretenberg, J., Żmihorski, M., Hiron, M. & Pärt, T. (2015) Linking occurrence and changes in local abundance of farmland bird species to landscape composition and land-use changes. *Agriculture, Ecosystems & Environment*, **204**, 1–7.

BirdLife International (2015) *European Red List of Birds*. Luxembourg.

BirdLife International (2016) IUCN Red List for Birds, www.birdlife.org

Brady, M., Kellermann, K., Sahrbacher, C. & Jelinek, L. (2009) Impacts of decoupled agricultural support on farm structure, biodiversity and landscape mosaic: some EU results. *Journal of Agricultural Economics*, **60**, 563–585.

Bravo, C., Ponce, C., Palacín, C. & Carlos Alonso, J. (2012) Diet of young Great Bustards *Otis*

tarda in Spain: sexual and seasonal differences. *Bird Study*, **59**, 243–251.

Bretagnolle, V., Villers, A., Denonfoux, L., Cornulier, T., Inchausti, P. & Badenhausser, I. (2011) Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme. *Ibis*, **153**, 4–13.

Burnham, K.P. & Anderson, R.P. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33**, 261–304.

Burnside, R.J., Végvári, Z., James, R., Konyhás, S., Kovács, G. & Székely, T. (2014) Human disturbance and conspecifics influence display site selection by great bustards *Otis tarda*. *Bird Conservation International*, **24**, 32–44.

Caballero, R., Fernández-gonzález, F., Badia, R.P., Molle, G., Roggero, P.P., Bagella, S., Ottavio, P.D., Papanastasis, V.P., Fotiadis, G., Sidiropoulou, A. & Ispikoudis, I. (2009) Grazing systems and biodiversity in Mediterranean areas : Spain, Italy and Greece. *Pastos*, **39**, 9–152.

Cabanillas, F.J.J., Aliseda, J.M. & Gallego, J.A.G. (2012) Land cover and land use change in the central Spanish-Portuguese border region. *Boletín de la Asociación de Geógrafos Españoles*, **60**, 369–398.

Chamberlain, D.E. & Fuller, R.J. (2000) Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. *Agriculture, Ecosystems & Environment*, **78**, 1–17.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 771–788.

Corbacho, C., Fernández, E., Costillo, E., Lozano, A. & Gil, A. (2005) La avutarda común en Extremadura: distribución, población y tendencias. *La Avutarda Comun en la Peninsula Iberica: Poblacion Actual y Metodo de Censo* (eds J.C. Alonso, C. Palacín, & C.A. Martín), pp. 34–43. SEO/BirdLife, Madrid.

Correal, E., Robledo, A., Ríos, S. & Rivera, D. (2003) Mediterranean dryland mixed sheep-cereal systems. *Grassland Science in Europe*, **11**, 2–4.

Debano, S.J. (2006) Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona. *Biodiversity and Conservation*, **15**, 2547–2564.

Dennis, P., Skartveit, J., Mccracken, D.I., Pakeman, R.J., Beaton, K., Kunaver, A. & Evans,

D.M. (2008) The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology*, **45**, 279–287.

Díaz, M., Naveso, M.A. & Rebollo, E. (1993) Respuesta de las comunidades nidificantes de aves a la intensificación agrícola en cultivos cerealistas de la Meseta Norte (Valladolid-Palencia, España). *Aegypius*, **11**, 1–6.

Donald, P.F., Pisano, G., Rayment, M.D. & Pain, D.J. (2002) The common agricultural policy, EU enlargement and the conservation of Europe's farmland birds. *Agriculture, Ecosystems and Environment*, **89**, 167–182.

Donald, P.F., Sanderson, F.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. *Agriculture, Ecosystems and Environment*, **116**, 189–196.

Drewitt, A.L. & Langston, R.H.W. (2008) Collision effects of wind-power generators and other obstacles on birds. *Annals of the New York Academy of Sciences*, **1134**, 233–66.

European Environment Agency (2007) *CLC2006 Technical Guidelines*.

Faria, N., Morales, M.B. & Rabaça, J.E. (2016a) Between and within-year effects of haying on grassland bird populations and spatial dynamics. *Agriculture, Ecosystems & Environment*, **220**, 193–201.

Faria, N., Morales, M.B. & Rabaça, J.E. (2016b) Exploring nest destruction and bird mortality in mown Mediterranean dry grasslands: an increasing threat to grassland bird conservation. *European Journal of Wildlife Research*, **62**.

Foley, J. A, Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E. A, Kucharik, C.J., Monfreda, C., Patz, J. A, Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570–574.

García-Llamas, P., Calvo, L., Álvarez-Martínez, J.M. & Suárez-Seoane, S. (2016) Using remote sensing products to classify landscape. A multi-spatial resolution approach. *International Journal of Applied Earth Observation and Geoinformation*, **50**, 95–105.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B., … Inchausti, P. (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, **11**, 97–105. doi:10.1016/j.baae.2009.12.001

Gewalt, W. (1959) *Die Grosstrappe*. Neue Brehm Bücherei, Wittenberg-Lutherstadt.

Gilroy, J.J., Anderson, G.Q.A., Vickery, J.A., Grice, P. V & Sutherland, W.J. (2011) Identifying mismatches between habitat selection and habitat quality in a ground-nesting farmland bird. *Animal Conservation*, **14**, 620–629.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005) Farming and the fate of wild nature. *Science*, **307**, 550–5.

Green, R.E., Tyler, G.A., Stowe, T.J. & Newton, A. V. (1997) A simulation model of the effect of mowing of agricultural grassland on the breeding success of the corncrake (*Crex crex*). *Journal of Zoology*, **243**, 81–115.

Grüebler, M.U., Schuler, H., Müller, M., Spaar, R., Horch, P. & Naef-Daenzer, B. (2008) Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. *Biological Conservation*, **141**, 3040–3049.

Haas, D., Nipkow, M., Fiedler, G., Schneider, R., Haas, W. & Schürenberg, B. (2005) *Protecting Birds from Powerlines*. NABU - German Society for Nature Conservation.

Hale, R. & Swearer, S.E. (2016) Ecological traps: Current evidence and future directions. *Proceedings of the Royal Society B-Biological Sciences*, **283**, 20152647.

Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS biology*, **5**, 1211–1219.

Jones, N., de Graaff, J., Rodrigo, I. & Duarte, F. (2011) Historical review of land use changes in Portugal (before and after EU integration in 1986) and their implications for land degradation and conservation, with a focus on Centro and Alentejo regions. *Applied Geography*, **31**, 1036–1048.

Kamp, J., Urazaliev, R., Balmford, A., Donald, P.F., Green, R.E., Lamb, A.J. & Phalan, B. (2015) Agricultural development and the conservation of avian biodiversity on the Eurasian steppes : A comparison of land-sparing and land-sharing approaches. *Journal of Applied Ecology*, **52**, 1578–1587.

Krebs, C.J. (2001) *Ecology*, 5th ed. Benjamin Cummings, San Francisco.

Lane, S.J., Alonso, J.C., Alonso, J.A. & Naveso, M.A. (1999) Seasonal changes in diet and diet selection of great bustards (*Otis t. tarda*) in north-west Spain. *Journal of Zoology*, **247**, 201–214.

Lane, S.J., Alonso, J.C. & Martín, C.A. (2001) Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas

unoccupied? *Journal of Applied Ecology*, **38**, 193–203.

Magaña, M., Alonso, J.C., Martín, C.A., Bautista, L.M. & Martín, B. (2010) Nest-site selection by great bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis*, **152**, 77–89.

Matthews, A. (2013). Greening agricultural payments in the EU's Common Agricultural Policy. *Bio-Based and Applied Economics*, **2,** 1–27.

Martín, C.A., Alonso, J.C., Alonso, J.A., Palacín, C., Magaña, M. & Martín, B. (2007) Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard *Otis tarda*. *Journal of Avian Biology*, **38**, 335–346.

Martín, B., Alonso, J.C., Martín, C. a., Palacín, C., Magaña, M. & Alonso, J.A. (2012a) Influence of spatial heterogeneity and temporal variability in habitat selection: A case study on a great bustard metapopulation. *Ecological Modelling*, **228**, 39–48.

Martín, C.A., Martínez, C., Bautista, L.M. & Martín, B. (2012b) Population increase of the great bustard *Otis tarda* in its main distribution area in relation to changes in farming practices. *Ardeola*, **59**, 31–42.

Moreira, F., Morgado, R. & Arthur, S. (2004) Great bustard Otis tarda habitat selection in relation to agricultural use in southern Portugal. *Wildlife Biology*, **10**, 251–260.

O'Neill, K.M., Olson, B.E., Rolston, M.G., Wallander, R., Larson, D.P. & Seibert, C.E. (2003) Effects of livestock grazing on rangeland grasshopper (Orthoptera: Acrididae) abundance. *Agriculture, Ecosystems and Environment*, **97**, 51–64.

O'Neill, K.M., Olson, B.E., Wallander, R. & Rolston, M.G. (2010) Effects of livestock grazing on grasshopper abundance on a native rangeland in Montana. *Environmental Entomology*, **39**, 775–786.

Olea, L. & Miguel-Ayanz, A.S. (2006) The Spanish dehesa. A traditional Mediterranean silvopastoral system linking production and nature conservation. *21st General Meeting of the European Grassland Federation. Badajoz (Spain)*, pp. 1–15.

Palacín, C., Alonso, J.C., Martín, C.A. & Alonso, J.A. (2016) Changes in bird-migration patterns associated with human-induced mortality. *Conservation Biology*, **31**, 106–115.

Patten, M.A., Wolfe, D.H., Shochat, E. & Sherrod, S.K. (2005) Habitat fragmentation, rapid evolution and population persistence. *Evolutionary Ecology Research*, **7**, 235–249.

Pimm, S.L. & Raven, P. (2000) Extinction by numbers. *Nature*, **403**, 843–845.

Pinto, M., Rocha, P. & Moreira, F. (2005) Long-term trends in great bustard (*Otis tarda*) populations in Portugal suggest concentration in single high quality area. *Biological Conservation*, **124**, 415–423.

Raab, R., Spakovszky, P., Julius, E., Schütz, C. & Schulze, C.H. (2010) Effects of power lines on flight behaviour of the West-Pannonian great bustard *Otis tarda* population. *Bird Conservation International*, **21**, 142–155.

R Core Team (2017) R: a language and environment for statistical computing, http://www.r-project.org/.

Reif, J., Vorišek, P., Štastný, K., Bejček, V. & Petr, J. (2008) Agricultural intensification and farmland birds: New insights from a central European country. *Ibis*, **150**, 596–605.

Reino, L., Porto, M., Morgado, R., Moreira, F., Fabião, A., Santana, J., Delgado, A., Gordinho, L., Cal, J. & Beja, P. (2010) Effects of changed grazing regimes and habitat fragmentation on Mediterranean grassland birds. *Agriculture, Ecosystems and Environment*, **138**, 27–34.

Ribeiro, P.F., Santos, J.L., Bugalho, M.N., Santana, J., Reino, L., Beja, P. & Moreira, F. (2014) Modelling farming system dynamics in High Nature Value Farmland under policy change. *Agriculture, Ecosystems and Environment*, **183**, 138–144.

Rocha, P., Marques, A.T. & Moreira, F. (2005) Seasonal variation in Great Bustard *Otis tarda* diet in south Portugal with a focus on the animal component. *Ardeola*, **52**, 371–376.

Rocha, P., Morales, M.B. & Moreira, F. (2012) Nest site habitat selection and nesting performance of the great bustard *Otis tarda* in southern Portugal: implications for conservation. *Bird Conservation International*, **23**, 323–336.

Salamolard, M. & Moreau, C. (1999) Habitat selection by little bustard *Tetrax tetrax* in a cultivated area of France. *Bird Study*, **46**, 25–33.

Sánchez, A. & Garcia-Baquero, M.J. (2012) La avutarda en Badajoz: estabilidad, pero con matices. *Quercus*, **314**, 16–22.

Santana, J., Reino, L., Stoate, C., Borralho, R., Carvalho, C.R., Schindler, S., Moreira, F., Bugalho, M.N., Ribeiro, P.F., Santos, J.L., Vaz, A., Morgado, R., Porto, M. & Beja, P. (2014) Mixed effects of long-term conservation investment in Natura 2000 farmland. *Conservation Letters*, **7**, 467–477.

Sastre, P., Ponce, C., Palacín, C., Martín, C.A. & Alonso, J.C. (2009) Disturbances to great

bustards (*Otis tarda*) in central Spain: human activities, bird responses and management implications. *European Journal of Wildlife Research*, **55**, 425–432.

Southwood, T.R.E., May, R.M., Hassell, M.P. & Conway, G.R. (1974) Ecological strategies and population parameters. *The American Naturalist*, **108**, 791–804.

Stoate, C., Borralho, R. & Araújo, M. (2000) Factors affecting corn bunting *Miliaria calandra* abundance in a Portuguese agricultural landscape. *Agriculture, Ecosystems & Environment*, **77**, 219–226.

Suárez, F., Naveso, M.A. & De Juana, E. (1997) Farming in the drylands of Spain: Birds of the pseudosteppes. *Farming and Birds in Europe. The Common Agricultural Policy and its Implications for Bird Conservation.* (eds D.J. Pain & M.W. Pienkowski), pp. 297–330. Academic Press, San Diego.

Thompson, P.M. & Ollason, J.C. (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature*, **413**, 417–420.

Vadász, C. & Lóránt, M. (2014) Key mortality causes of the Great Bustard (*Otis tarda*) in Central Hungary: An analysis of known fatalities. *Ornis Hungarica*, **22**, 32–41.

Wolfe, D.H., Patten, M.A., Shochat, E., Pruett, C.L. & Sherrod, S.K. (2007) Causes and patterns of mortality in Lesser Prairie-chickens *Tympanuchus pallidicinctus* and implications for management. *Wildlife bi*, **13**, 95–104.

Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T. & Pärt, T. (2006) Population trends of farmland birds in Sweden and England: Similar trends but different patterns of agricultural intensification. *Journal of Applied Ecology*, **43**, 1110–1120.

Appendices

Appendix 3.1: Data on fence densities (n is number of 500 m transects) collected in spring 2017 in eight subpopulations.

Subpopulation	***Fence intersections / 500 m mean (SD), n***
Central Cáceres	*1.91 (1.92), n =141*
Campo Lugar	*2.06 (1.21), n=35*
Castro Verde	*1.41 (1.53), n=93*
Cuba	*0.48 (0.51), n=23*
Evora	*1.11 (0.96), n=18*
La Serena	*1.26 (0.97), n=116*
Montijo	*1.00 (1.05), n=63*
Northern Alentejo and western Badajoz	*1.36 (1.53), n=193*

Chapter 4

Is the Great Bustard a good surrogate for an agro-steppe bird assemblage?

4.1 Abstract

Indicating wider biodiversity using surrogate species is common practice in conservation with mixed effectiveness. Species with complex life histories and habitat-uses may function as appropriate indicators for assemblages comprising species with varying ecological requirements. The threatened Great Bustard (GB) is the only regularly-monitored species of agro-steppe bird-assemblages in Extremadura (Spain) and Alentejo (Portugal), and shows mixed trends across the region. This study tested whether GB is a good surrogate or indicator species for the agro-steppe species assemblage. Using generalised linear models and nonmetric multidimensional scaling, GB monitoring data and field surveys (956 point counts and 759 transects) for other agro-steppe species, and measurement of several environmental variables across a network of Special Protection Areas (SPAs) I show that GB is not a good predictor for richness of all breeding farmland species, for agro-steppe specialists and for species of conservation concern. Correlation coefficients between densities of 14 species and GB counts were not significant apart for Montagu's Harrier (r^2= 0.361, $p<0.05$). Several environmental variables—(a) land-cover types (cereals, pastures, stubbles and dry fields), (b) region and (c) presence of point count inside or outside SPA—were significantly linked with species assemblage composition. GB presence was not significantly correlated with species assemblage composition. Agro-steppe specialists and species of conservation concern (Little Bustard, Lesser Kestrel, Short-toed and Calandra Larks) were found in point counts more outside of SPAs, and were also associated with pastures and stubbles. In central Cáceres and eastern Badajoz several agro-steppe species were under-represented. Statistical links between abundances of different

species and several environmental factors were partially scale-dependent. This study suggests that GB may not act as a good or surrogate or indicator for the entire agro-steppe bird assemblage. Additional species need to be monitored regularly, to allow better understanding of changes in this important bird assemblage. This study also indicates that not all SPAs in Extremadura and Alentejo provide adequate conditions for agro-steppe species. A regional assessment of the function of SPAs, and of monitoring priorities, is needed.

4.2 Introduction

Indicator species are commonly used to monitor multi-taxa biodiversity status and change in response to environmental changes (e.g. Hansson 2000; Dale & Beyeler 2001; Gregory *et al.* 2005). The selection process of species that best represent multi-taxa has been widely addressed using different approaches (e.g. Roberge & Angelstam 2004; Siddig *et al.* 2016). Currently a niche-based approach to selecting a group of indicator species that cover the entire breadth of niches in a landscape is efficiently used in some large-scale bird monitoring schemes (Butler *et al.* 2012; Wade *et al.* 2014). Multi-species indices are often regarded as more useful to nature conservation than single-species indices, as they better indicate the true condition of the environment (Hansson 2000; Veríssimo *et al.* 2014). However, such monitoring programs need to be considered carefully as they can be costly, so single species are still in use as indicators, often because they are rare and endangered, or de facto treated as flagship or umbrella species (Lambeck 1997; Simberloff 1998). The effectiveness of using single bird species to indicate the status of a wider biota has seldom been studied, with ambiguous results in different landscapes and management intensities, almost exclusively in complex forest systems (see meta-analysis by Branton & Richardson 2011 and by Gao, Nielsen & Hedblom 2015). For example, Roberge & Angelstam (2006) showed that woodpecker species can be used to indicate richness and abundance of common forest bird species in northern Europe, but there was considerable variation among habitats and different levels of forest management in the effectiveness of the indicator species. More specifically, species richness of deciduous forest birds in central Sweden was 13% higher in atlas squares with White-backed Woodpecker

(*Dendrocopos leucotos*) than in squares without woodpeckers (Roberge, Mikusiński & Svensson 2008). Most studies on the effectiveness of single indicator bird species focused on species with simple life histories or did not address their complex life histories (e.g. Pakkala *et al.* 2014; Gao, Nielsen & Hedblom 2015). However, it may be instructive to study the use of species with complex life histories that result in complex multi-habitat requirements as surrogates for an assemblage of species with different habitat requirements. For example, the distribution of Capercaillie (*Tetrao urogallus*) was linked with mountain bird diversity but not with forest bird diversity in the Swiss Pre-alps (Suter, Graf & Hesst 2002), and no Capercaillie studies explicitly addressed its complex life history and use of multiple habitats.

Great Bustard (*Otis tarda*) is globally Vulnerable (BirdLife International, 2017a) and appears in Annex 1 of the European Birds Directive (2009/147/EC). In the past two decades a network of Natura 2000 agro-steppe Special Protection Areas (SPAs) and Special Areas of Conservation (SACs) in Extremadura (Spain) and Alentejo (Portugal) was set up under the European Birds Directive and the Habitats Directive (1992/43/EEC), to ensure favourable conservation status of Annex I species, by protecting areas where Great Bustards, Little Bustards (*Tetrax tetrax*) and Lesser Kestrels (*Falco naumanni*) were concentrated. The network aims to protect agro-steppe habitats mainly by mitigating agricultural intensification and development through legislation. Agro-environmental schemes set up to actively improve habitat quality have only been documented in Castro Verde in southern Alentejo (Santana *et al.* 2014). Elsewhere in Extremadura and Alentejo active conservation measures, if any, are probably local and undocumented.

Great Bustard (GB) biology in Iberia is intensively studied (see review in Alonso, 2014), because of its size and prominence, and because of its global Vulnerable conservation status (BirdLife International 2017a). Although it is not officially defined as an indicator or surrogate species in Extremadura and Alentejo, in practice, GB is the only agro-steppe species monitored regularly in Extremadura and Alentejo, and as such it may be assumed to act as an indicator species for other agro-steppe species. Additionally, elsewhere in Iberia, management of SPAs was directed more towards Great Bustard than other agro-steppe species (Moreno *et al.* 2010). GB has a complex life history, where both sexes utilize micro-habitats in the landscape differently, due to their different roles in the lekking breeding system: males often lek on low, sloping hills with good visibility and short grass (Alonso, Álvarez-Martínez & Palacín 2012) whereas females select sheltered micro-habitats with tall vegetation to breed (Magaña *et al.* 2010; Rocha, Morales & Moreira 2012). However, this sexual segregation in habitat selection is probably scale-dependent, as in a study in central Spain no niche partitioning was found between male and female Great Bustards (Traba *et al.* 2015). Therefore, it may be expected that in sites with high GB density all species that share these different micro-habitat requirements will be represented in good densities as well. This link between the density of an indicator species and the density of other species, through habitat requirements, may occur at varying spatial scales, based on the spatial scale at which species select their habitat (Pakkala *et al.* 2014).

Species coexsistence may be facilitated by different habitat selection at various spatial scales, and also by resource partitioning if resources are shared (Traba *et al.* 2015). GB has wide breeding habitat selection, not only due to sexual

differences. GB was found to favour fallows, similar to other agro-steppe species such as Eurasian Stone-curlew (*Burhinus oedicnemus*), Black-bellied Sandgrouse (*Pterocles orientalis*) and Calandra Lark (*Melanocorypha calandra*) (Delgado & Moreira 2000). GB was also found to select stubbles, cereals and pastures for breeding (Alonso, Álvarez-Martínez, & Palacín 2012; Lane, Alonso, & Martín 2001; Lopez-Jamar *et al.*, 2010; Magaña *et al*. 2010; Rocha, Morales, & Moreira 2012; Schwandner & Langgemach 2011). Habitat local-scale requirements of GB and Little Bustard were found to be different (Tarjuelo *et al.* 2014) and resource partitioning was found at microhabitat scale according to their body size (Traba *et al.* 2015). This scale-dependency of habitat links between GB and other agro-steppe species is a clear intimation that GB might be an imperfect indicator species for the entire agro-steppe bird assemblage. An overall evaluation of the Great Bustard as an indicator surrogate species for agro-steppe bird assemblage is necessary, especially in context of understanding the habitat preferences and resource partitioning with other species. It is also necessary to identify whether more agro-steppe species need to be monitored, or whether GB is a satisfactory indicator species for agro-steppe species. Using this information, bird monitoring priorities in this region may be evaluated. Additionally, understanding whether a complex life history species acts as a good indicator might provide an important scientific insight, and infer monitoring decisions in other systems. Because of its broad habitat use, I predict that GB is a good indicator species for the entire agro-steppe assemblage.

Little is known about the function of the Natura 2000 network across Extremadura and Alentejo to ensure favourable conditions for Annex 1 species, and few efforts are set towards monitoring other species of conservation concern in the

same agro-steppe assemblage. A recent study revealed that the Natura 2000 network in Alentejo did not prevent an overall 49% decline of Little Bustards between 2003–2006 and 2016 (Silva *et al.* 2018). In Castro Verde SPA, Alentejo, temporal changes in abundance of Great and Little Bustards and Lesser Kestrel were more favourable inside the SPA than outside, but the reverse was found for several other bird groups, including species of conservation concern (Santana *et al.* 2014). Additionally, implementation of agri-environmental measures in SPAs may benefit some agro-steppe species but not others, as suggested by an expert-opinion study in Spain (Moreno *et al.* 2010). An evaluation of the function of the SPA network in Extremadura and Alentejo in creating favourable conditions for unmonitored agro-steppe species is necessary. I predict that in SPAs, the agro-steppe bird species for which the network was declared will fare better.

This study examined whether GB is a good surrogate for other agro-steppe species, so sites that are good for Great Bustards are also good for other agro-steppe species and for the entire agro-steppe bird assemblage. More specifically, this study (a) tests whether GB counts are correlated with species richness of farmland breeding species, (b) relates GB counts to relative densities of individual species of this assemblage, and (c) relates patterns in assemblage composition to GB presence, land-cover types, vegetation structure, SPAs and differences between regions at multiple spatial scales.

4.3 Methods

4.3.1 Study area and sampling design

A description of the agricultural system in Extremadura and Alentejo is in Chapter 3. Predominately agro-steppe cells (n= 50, each 5 km x 5 km, 25 km^2) were pre-selected, distributed across the study area from southern Alentejo to central and eastern Cáceres (Fig. 4.1), according to their habitat, based on Corine Land Cover (Coordination of Information on the Environment Land Cover, CLC) 2012 and recent Google maps. In all cells, 50% or more of the cell area was identified as agro-steppe habitat: non-irrigated arable land (mainly cereals), and pastures and grasslands. Cells were stratified according to two attributes: (a) occurrence or absence of Great Bustards by intersecting cells with where Great Bustards were seen after 2010, and (b) whether the cell was inside or outside an SPA. Lack of data prevented the creation of a metric to describe the levels of conservation efforts applied in different SPAs, so whether the cell was inside and SPA or not was used as an index for conservation efforts, acknowledging the limitations of this index. In addition to their attributes mentioned above, cells were selected according to their limited availability – there were very few available cells outside SPAs and without Great Bustards. Inside SPAs, where GB occurred, cells were selected to provide complete coverage of SPAs, bringing into account access issues (private properties and availability of paved tracks).

In the field, the dominance of agro-steppe habitat was verified visually and using knowledge of local experts. Ten pre-selected cells were not surveyed, two due to access difficulties and eight due to recent conversion to irrigated or permanent crops which decreased the area of agro-steppe habitat in the cell below

50%. However, five cells that were pre-identified as agro-steppe but not initially selected were surveyed as well, after field verification that they included 50% or more agro-steppe habitat and had good access. In total, 45 cells were surveyed, of which 29 cells had Great Bustards and 16 cells did not; and involving 26 cells inside SPAs and 19 cells outside SPAs (Fig. 4.1). Both bird and habitat data (see below) were recorded in the field using a free, bespoke app designed on Survey123 platform (ESRI 2017).

The sampling effort included point counts (PC) and line transects, which recorded both birds and habitat. PC and transects were located within cells in or bordering agro-steppe habitats only, in pre-selected positions, to represent the relative proportionate extent of CLC 2012 non-irrigated arable land, grasslands and pastures. The number of PC and transects per cell in each of the land-cover types was proportionate to the relative area of that land-cover type out of the entire agro-steppe habitat in the cell.

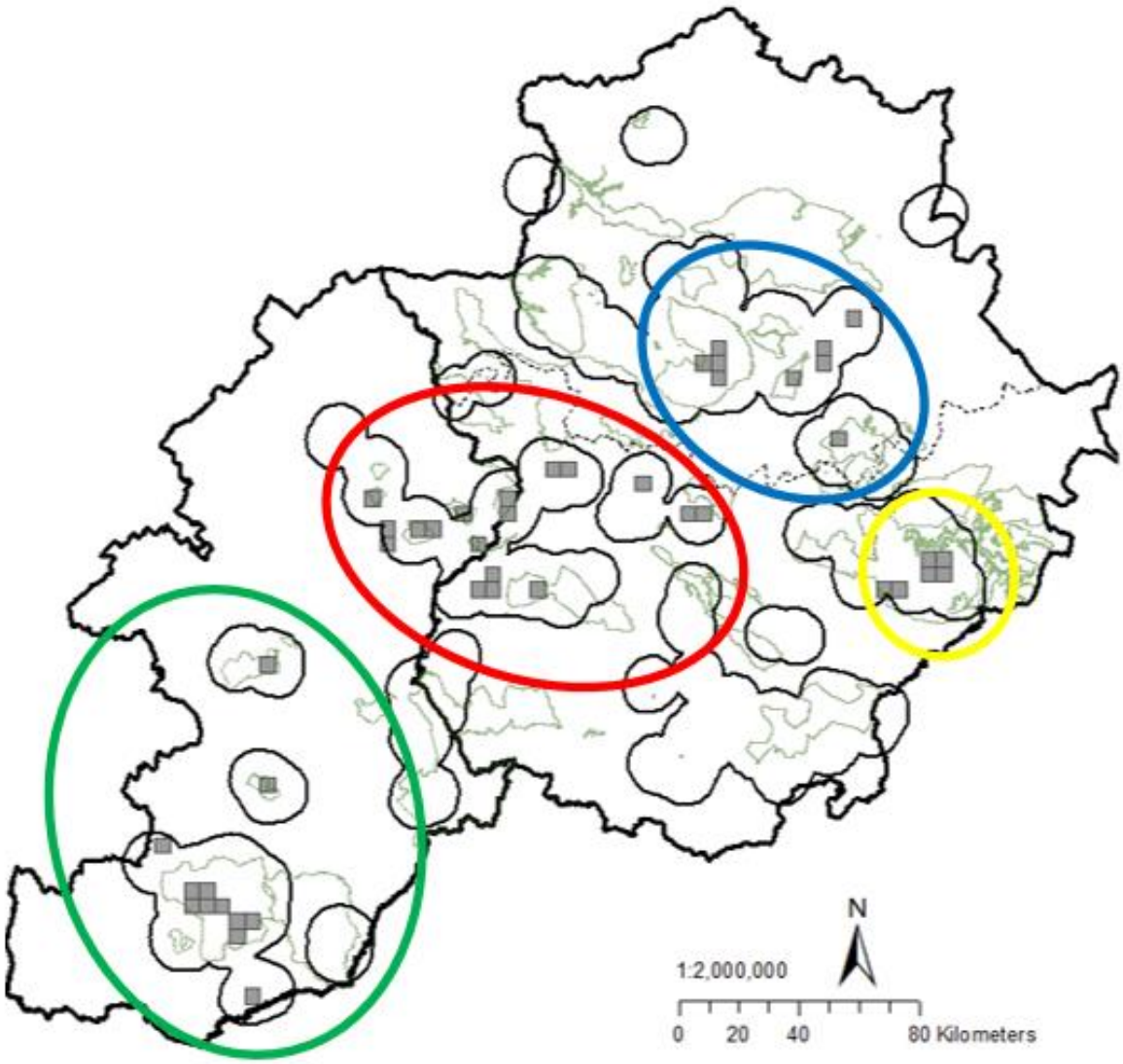


Figure 4.1: Study area in Extremadura (Spain) and Alentejo (Portugal). Thick black lines are outer boundaries of Extremadura and Alentejo. Dashed line is provincial boundary between Cáceres and Badajoz. Grey rectangles are 25 km^2 cells surveyed in spring 2017. Polygons with pale green outline are agro-steppe SPAs (ZEPA in Spain, ZPE in Portugal). Thin black lines are Great Bustard subpopulations as defined in Chapter 2. Colour circles represent regions. Blue – central Cáceres. Yellow – eastern Badajoz. Red – northern Alentejo and western Badajoz. Green - southern Alentejo. These regions correspond with Figures 4.4a-b.

4.3.2 Bird surveys

Fieldwork was carried out between 10 April and 20 May 2017. In each 25 km^2 cell, bird counts (PC and transects) were used to collect data on breeding bird species. Bird counts started 30 minutes after first light, and extended up to four hours (less if heat load was too heavy), in order to maximize the number of PC and transects, until heat load reduced bird activity. Bird counts recommenced two hours before sunset, and finished before dusk when diminishing light prevented bird detection. They were carried out by three observers using binoculars and vocal cues after group training in the field and calibration of field methods. PC were at least 500 m from each other, to ensure their independence. Similarly, transects were between point counts, at least 500 m between end point of one transect to start point of the next, to ensure their independence. To avoid damage to crops or risk of encounter with livestock, PC and transects were conducted on dirt tracks.

In each cell, a mean of 21.2 points counts were carried out (total=956, range=9–31, SD=4.5). PC focused on terrestrial agro-steppe species – Little Bustard, Red-legged Partridge (*Alectoris rufa*), Stone Curlew (*Burhinus oedicnemus*), Lesser Kestrel, Calandra Lark (*Melanocorypha calandra*), Short-toed Lark (*Calandrella brachydactyla*), Thekla Lark (*Galerida theklae*), Zitting Cisticola (*Cisticola juncidis*) and Corn Bunting (*Emberiza calandra*), but all species seen during PC were recorded. Each point count lasted 5 minutes, and surveyed a circle with a radius of 125 m from central point (area= 49087 m^2). Within this radius, all birds were identified and counted and the distance to each individual bird was measured using Nikon Coolshot 20™ rangefinder, accurate to the distance of 500 m. Because of their larger territory size, Little Bustards were recorded up to 300 m. Recently-

fledged juveniles were excluded from counts. At each point count, wind speed (categorical: no wind, light, strong) and precipitation (categorical: dry, light rain, heavy rain) were recorded. However, fieldwork was not conducted in conditions of substantial rain or strong wind.

In addition to PC, in each cell a mean of 16.9 line transects of 500 m (total=759, range=5–26 SD=5.0) were surveyed, primarily to increase encounter probabilities of three scarce and mobile species, i.e. Montagu's Harrier (*Circus pygargus*), Pin-tailed Sandgrouse (*Pterocles alchata*) and Black-bellied Sandgrouse. To record these species, it was essential to add this different method as PC could under-record these species. As these species are normally seen in flight, not necessarily utilising habitats below them, habitat was not recorded along the transect. Along each transect, all individuals of the three target species were located, identified and counted, and the perpendicular distance to each individual measured up to 500 m. If a bird was flying towards or away from the transect, the nearest distance of its flight trajectory to the transect was recorded.

Although GB are best monitored in late March and early April (see count design and methods in Chapter 2, Alonso *et al.* 2005), they were visible also at large distances during fieldwork for this study. GB were noted and counted both in PC and transects, also beyond the PC radius and transect boundary. A total GB count per cell was noted, accumulating all individuals observed by all observers in the cell. Observers communicated using radio and phone to avoid double-counts of GB. GB cell totals in 2017 fieldwork were correlated against 2012–2014 mean count per cell (count methods as described in Chapter 2). Although well correlated (results of

correlation between GB cell count in 2017 and GB cell mean count 2012–2014: $\log_{10}$ [GB cell count late spring 2017] = 0.471* $\log_{10}$ [GB cell mean of early spring count 2012–2014] + 0.228; t=4.162, df=33, P<0.0001, r=0.587), and there was a 100% match between where GB were present or absent in 2017 and in 2012–2014, 2017 counts underestimated 2012–2014 mean counts. Therefore, for this study, GB mean counts 2012–2014 were regarded as more reliable, even though a decline might have occurred in some subpopulations between 2014 and 2017 that may account for at least part of the underestimation of 2017 GB counts (see Chapters 2 and 5). Mean counts in 2012–2014 were used for further analyses, acknowledging the problematic use of data from different years in the analyses.

In every 25 km^2 cell, a mean 37.9% (SD=10.6, range=13.5-58.1) of total cell area was physically sampled for birds, combining the area of PC and transects. Therefore, the combination of PC and transects in cells provided a representative picture of the bird assemblages and habitats (see below) in each cell.

4.3.4 Habitat measurements

Habitat was recorded visually in all 125 m radius PC using a dominance index of land-cover types (agro-steppe components: cereals, pasture, stubble (recently harvested cereals), dry field, fallow, other land-cover types: olive, vineyard, scrub, and other less frequent types), visually recording the number out of eight equal segments of PC in which the habitat type was dominant. Additionally, in each segment, mean sward height was visually estimated to the nearest 10 cm, and ground cover was visually estimated to the nearest 10%.

4.3.5 Data analysis

In order to test whether GB annual counts predicted cell species richness, generalised linear models (GLMs) relating cell species richness (eight cells from Castro Verde were excluded as annual GB counts were not explicitly available, n=37; species counted in PC and transects, relative to number of PC and transects in that cell) to GB mean cell count, season effect (number of weeks after start of fieldwork, 1 to 6, continuous) and geographic gradient (a straight line between the southwesterly corner of the study area and the northeasterly corner was drawn; for each cell centroid, a perpendicular line was drawn to the southwesterly-northeasterly line; the distance in km from the southwesterly bottom of the line to the intersection of the two lines was used) were compared with null models. This analysis was repeated separately for all breeding farmland species, agro-steppe specialists (in accordance with Suarez *et al.* 1997), and conservation concern species (IUCN and EU; BirdLife International 2015, 2017b). Using multimodel inference methods with package MuMIn (Bartoń 2013), best supported models were selected based on changes in Akaike information criterion (AICc) values, when decrease of 2 AICc values or more compared to simpler models indicated strong support (Burnham & Anderson 2004). Potential spatial autocorrelation in richness similarity between cells was tested using Moran's-I in R package spdep (Bivand & Piras 2015).

Using DISTANCE package in R (Miller 2017), densities of 14 species in point counts (12 species recorded in PC, 2 in transects) were calculated by compensating for detectability biases. These 14 species selected had sufficient non-zero counts (60 counts or more, Buckland *et al.* 2005, Appendix 4.1) to produce valid DISTANCE

models. Potential detectability variables that were initially brought into the analyses included observer (categorical, three observers), morning or evening (categorical), hours after dawn / hours before dusk (integer, 1 to 4), week after start (integer, 1 to 6), sward height (strongly correlated with ground cover, contonuous) and wind (categorical, yes/no). Rain was excluded as it was recorded only in two PC. For each species, models including each one of these variables separately were compared with null models based on changes in AICc values. Sample size was not large enough to produce valid results using a full model. For each species, variables whose statistical link with bird numbers were not strongly supported were removed from subsequent analyses. A similar process was repeated for transect-only species (excluding sward height as a detectability variable, as habitat was not recorded along transects), to produce density of each species per transect and per cell. For all species, hazard-rate detection function performed better than half-normal, and was selected.

To bring together density data of species recorded in PC and species recorded on transects, I generated standardised mean cell density values. Rather than using DISTANCE-generated density values directly, for each species z-transformations were used as metric for density, relating the standard deviation of each observation to the difference between observation and the mean density of that species across all PC (Z-score=(observation-mean)/standard deviation). This generated standardised mean cell density values (i.e. z-scores). In order to test whether GB mean count was linked with densities of single species, using correlation models, the correlation coefficient (r) of each species' cell density (n=37) with GB mean count was computed. In a graph presenting the relationship

between species mean cell density and GB mean count, 14 species are organised by subsets (all species, agro-steppe specialists, and species of conservation concern), and along a habitat gradient from scrub specialists to bare ground specialists. Information on species habitat preferences was obtained from BirdLife International (2017b).

In order to visually explore patterns in assemblage composition, assemblage composition was examined using nonmetric multidimensional scaling (NMDS) performed on a matrix of Bray-Curtis dissimilarities of DISTANCE-generated abundance data, in R package Vegan (Oksanen *et al.* 2017). For this analysis, 12 most frequent species recorded in PC were included. Because responses of different bird species to environmental variables are expected at different spatial scales, visualisations of dissimilarities in species assemblage were carried out, between PC (n=955) where results are for birds counted within the PC area, and between 25 km^2 cells (n=45) where both bird abundances and environmental variables were averaged across the cell (because PC design in cell represented CLC2012 agro-steppe habitats in the cell, mean of environmental variables recorded in PC represents the habitat at cell-scale). Dissimilarities in assemblage composition were plotted as two-dimensional distances along unconstrained ordination axes. Ordinations with stress value of below 0.2 were considered meaningful (Clarke & Warwick 1994).

In order to identify which environmental factors shape assemblage composition, function envfit in Vegan was used to fit potentially significant environmental and geographic factors onto ordinations, by plotting the best

correlation between NMDS ordinations and environmental variables. The following environmental and geographic variables were fitted onto ordinations (at PC scale and at cell scale) using (999 permutations): (a) dominance of land-cover types that appeared in more than 10% of PC (between 0 and 8, continuous: pasture, cereal, stubble, olive, dry field, legume and scrub), (b) region (4 regions; factorial), (c) overlap with Great Bustard subpopulations (yes/no), (d) SPA legislation (yes/no), (e) mean ground cover (continuous) and (f) habitat complexity (number of different land-cover types within PC area, continuous). The importance of geographic variables (region) was evaluated by partitioning variance explained by habitat variables (land-cover types, habitat complexity and ground cover) from variance explained by geographic variables, following an approach developed by Borcard, Legendre & Drapeau (1992). To determine which environmental factors significantly correlated with NMDS ordinations, correlations (r^2) of the cosine vector of each environmental and geographic variable with NMDS ordinations were computed.

Environmental variables that were significantly correlated with NMDS ordinations were used in a series of single-species GLMs, relating the abundance of each species per PC and per 25 km^2 cell to those environmental factors. The large number of variables resulted in hundreds of models to assess, of which many models were within 2 AICc values from top models. To identify variables which have overall stronger predictive power, model averaging was used to identify the mean effect sizes of environmental variables. In this procedure, effect sizes and standard errors of variables in the all models that received the strongest support (within 2 AICc values of the model with the lowest AICc) were averaged.

All analyses were done in R version 1.0.136 (R Core Team 2017).

4.4 Results

In all PC and transects, a total of 98 species were encountered. Of them, 42 were potentially breeding farmland species (Appendix 4.1). Species richness, controlled for sampling effort per cell, varied between cells: out of 42 farmland species, a cell mean of 20.32 (SD=3.17, range 15–26) were seen; agro-steppe specialists 10.08 (1.72, 6–13); species of conservation concern 11.95 (2.22, 7–16; Table 4.1).

Table 4.1: Total, mean (and SD) species richness per 25 km^2 cell of breeding farmland birds in Extremadura and Alentejo, April–May 2017.

	All farmland species	***Agro-steppe specialists***	***Species of conservation concern***	***Number of samples (PC & transects)***
Total number of species in all cells	*42*	*16*	*24*	
Mean number per cell	*20.32*	*10.08*	*11.95*	*39.38*
Range	*15–26*	*6–13*	*7–16*	*23–57*
SD	*3.17*	*1.72*	*2.22*	*8.24*

No support was found for models relating cell species richness per sample to GB mean counts 2012–2014 (square-rooted). AICc values of models including GB counts were not distant enough from the null model in all three species subsets to consider GB as supported predictor (all species, agro-steppe specialists and species of conservation concern; Figs. 4.2a-c, Tables 4.2a-c). No spatial autocorrelation was found between species richness in cells (Moran's I index=-0.04, p=0.415), implying that richness in cells was spatially randomly distributed.

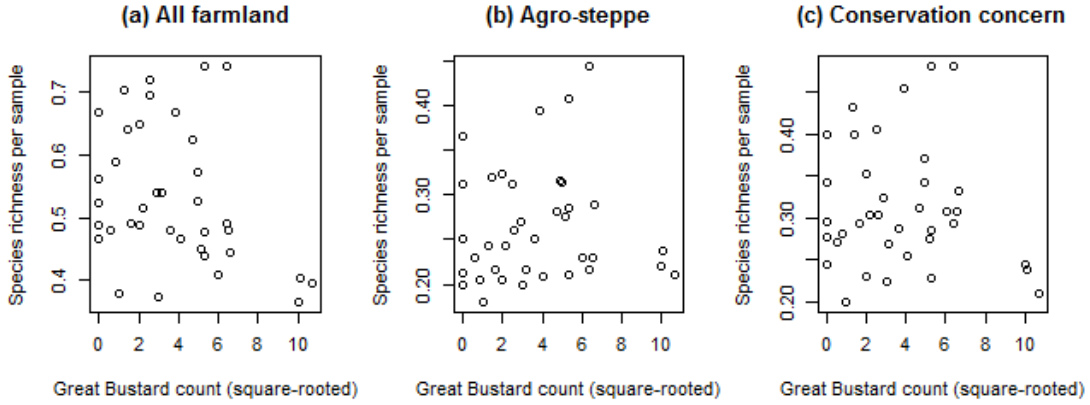


Figure 4.2a-c: Links between species richness per sample (point count or transect) in 25 km^2 cells across Extremadura and Alentejo, April–May 2017, and Great Bustard mean counts (square rooted) in the years 2012–2014, in those same cells. Correlations were examined for three species subsets: (a) all breeding farmland species, (b) agro-steppe specialists, and (c) species of conservation concern. Correlations of all three species subsets were not significant.

Table 4.2a-c: Results of generalised linear models relating species richness of: 3a: all farmland species; 3b: agro-steppe specialist species; 3c: species of conservation concern) per 25 km^2 cell in Extremadura and Alentejo, April–May 2017, showing parameter estimates (SE). Models ranked by AICc; best-supported model shown in **bold**.

Table 4.2a: All farmland species

Model	*Great Bustard (square-rooted)*	*Week*	*Location*	*df*	*AICc*	*ΔAICc*
1	*-0.012(0.006)*	*-0.017(0.020)*		*34*	*-55.43*	*0*
2 (Null)				***36***	***-55.50***	***0.07***
3	*-0.012(0.006)*		*>-0.001(<0.001)*	*34*	*-55.52*	*0.09*
4	*-0.012(0.006)*	*-0.008(0.031)*	*>-0.001(<0.001)*	*33*	*-52.90*	*2.53*

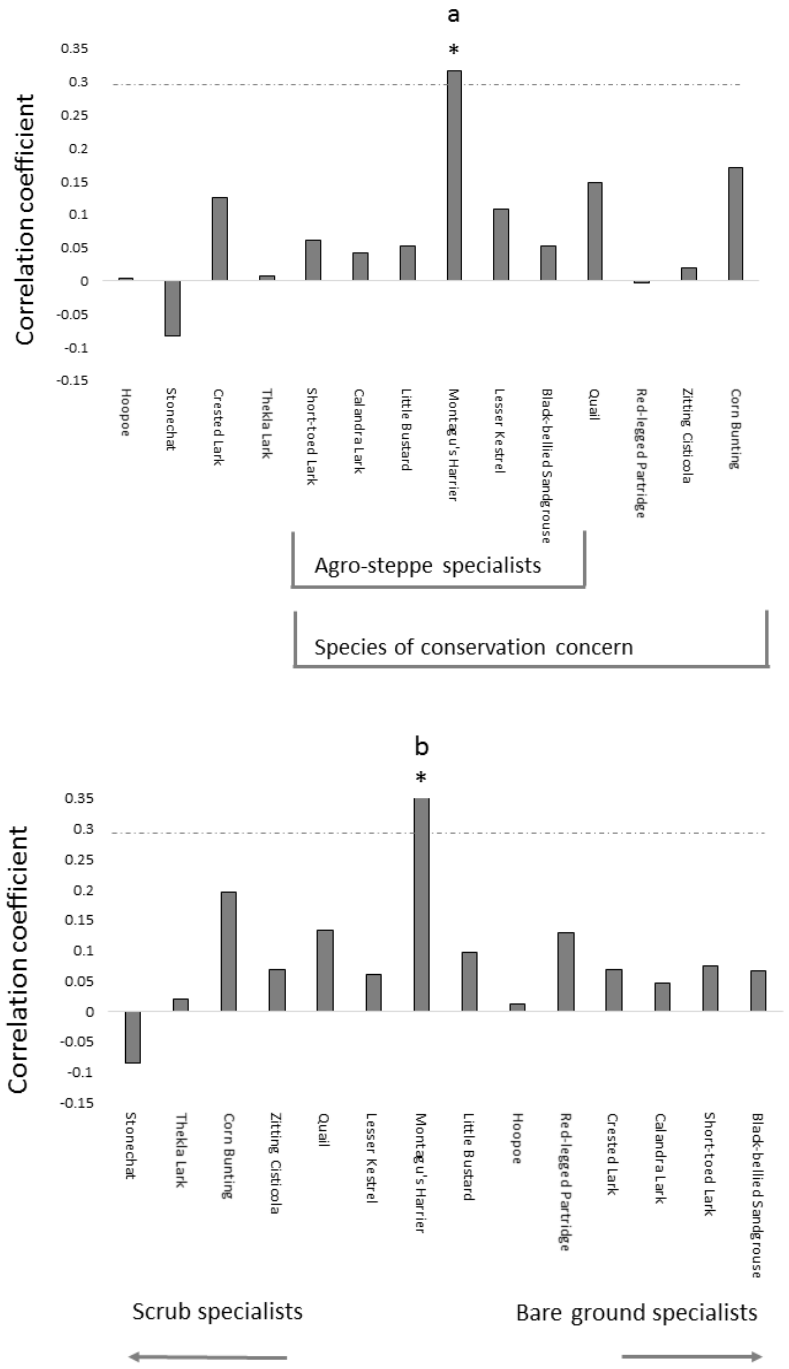
Table 4.2b: Agro-steppe specialists

Model	*Great Bustard (square-rooted)*	*Week*	*Location*	*df*	*AICc*	*ΔAICc*
1 (Null)				***36***	***-95.31***	***0***
2	*0.001(0.004)*		*>-0.001(<0.001)*	*34*	*-91.49*	*3.82*
3	*0.001(0.004)*	*-0.006(0.012)*		*34*	*-90.78*	*4.53*
4	*0.002(0.004)*	*0.006(0.019)*	*>-0.001(<0.001)*	*33*	*-88.92*	*6.39*

Table 4.2c: species of conservation concern

Model	*Great Bustard (square-rooted)*	*Week*	*Location*	*df*	*AICc*	*ΔAICc*
1 (Null)				***36***	***-84.64***	***0***
2	*-0.002(0.004)*		*>-0.001(<0.001)*	*34*	*-82.45*	*2.19*
3	*-0.003(0.004)*	*-0.017(0.014)*		*34*	*-81.90*	*2.74*
4	*-0.002(0.044)*	*-0.005(0.022)*	*>-0.001(<0.001)*	*33*	*-79.83*	*4.81*

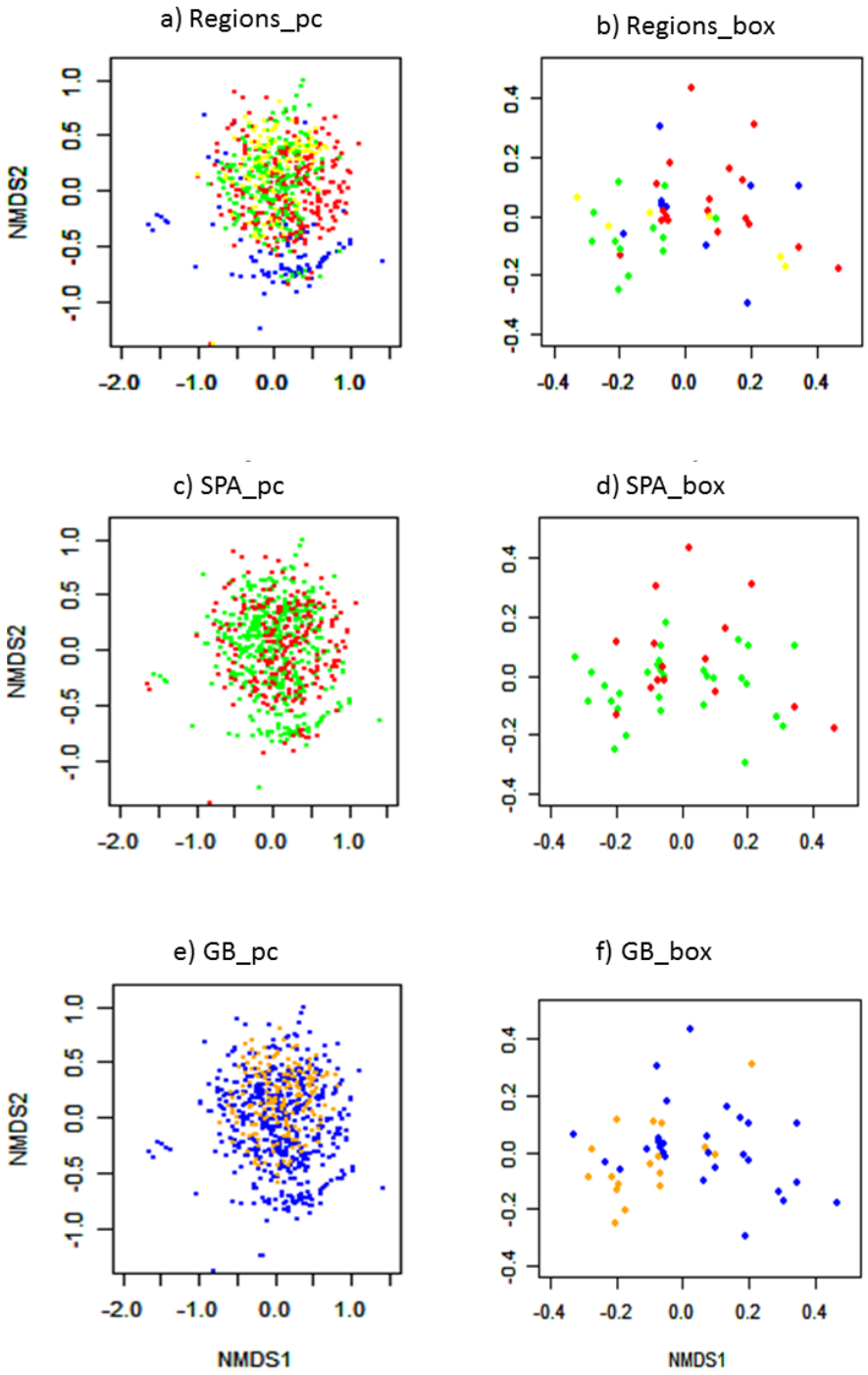
When comparing the correlation coefficients between z-scores (based on DISTANCE-generated density) of 14 species, in different species classifications, and GB mean count, no overall pattern was found, and for almost all species correlations were not significant: only Montagu's Harrier's density was significantly correlated to GB mean count ($t= 2.536$, $r=0.361$, $p<0.05$, Figs. 4.3a-b).



Figures 4.3a and 4.3b: Correlation coefficients between densities of single species in 25 km^2 cells across Extremadura and Alentejo, April–May 2017, and Great Bustard mean counts in the years 2012–2014, in those same cells. Dashed line is expected r to achieve p=0.05. Species are ranked according to two gradients or subsets: (a) agro-steppe specialists, species of conservation concern, all breeding farmland species, (b) gradient from scrub specialists, through cereal and pasture species, to bare ground specialists. Information on species habitat preferences is from BirdLife International (2017b).

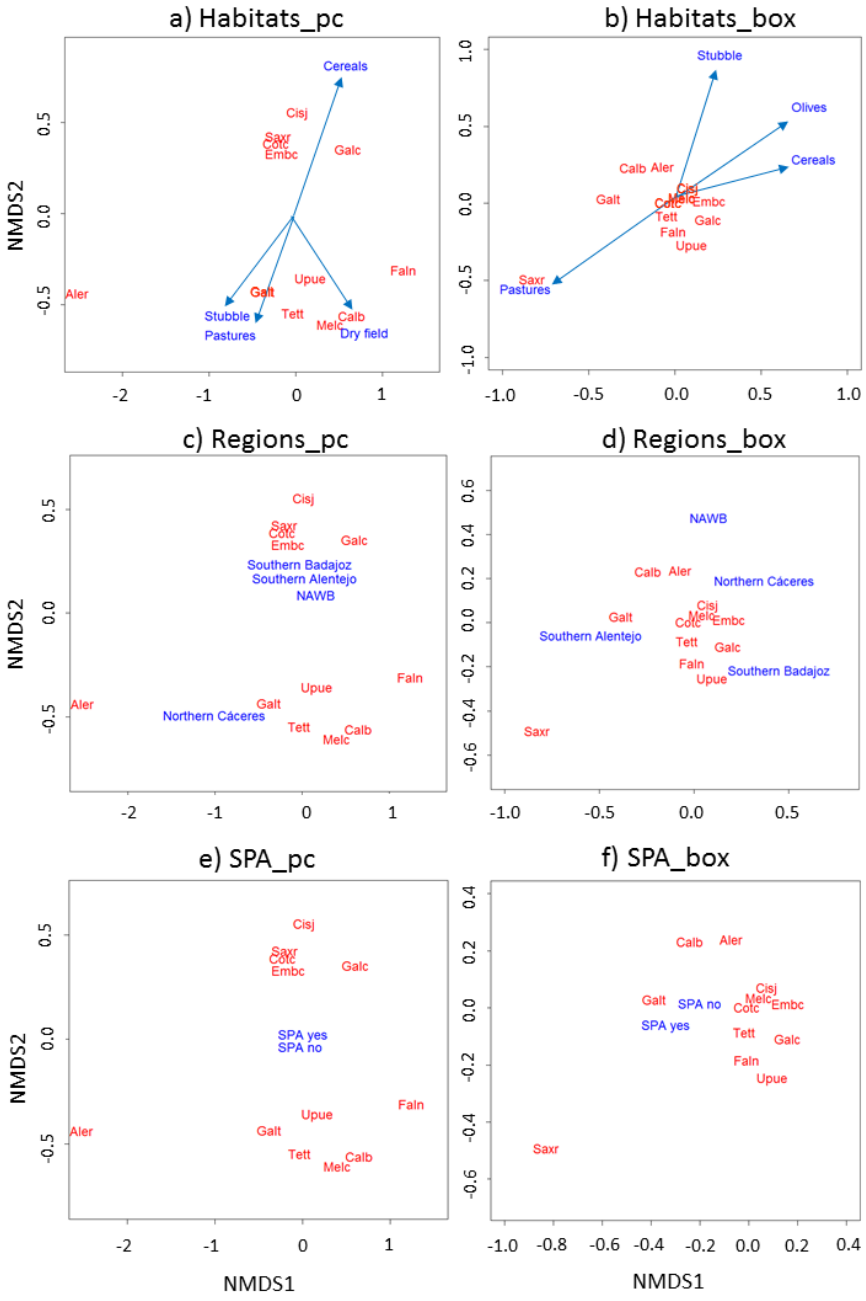
Results of NMDS ordinations, visualising the Bray-Curtis dissimilarities in species assemblages between PC, demonstrated that species assemblages of most PC were clustered together (Figs. 4.4 a,c,e). NMDS models had a good explanatory power: stress value was 0.18 for models using PC as replication, and 0.17 for models using 25 km^2 cell as replication, and NMDS ordinations were correlated with NMDS axes ('raw' data versus 'summary') with r^2=0.43 and R^2=0.62 respectively.

Variance (r^2) explained by geographic variables (region) solely was 25.17% at PC scale, and 12.17% at cell scale; therefore, region was included in envfit analyses at both scales. Environmental and geographic factors that were found to be significantly correlated with NMDS ordinations (the distances between PC; Table 4.3, Figs. 4.4a,c,e and 4.5a,c,e) were cereals (r^2=0.015, p<0.001), stubbles (r^2=0.012, P<0.01), pastures (r^2=0.007, p<0.05), dry field (r^2=0.006, p<0.05), region (r^2=0.031, p<0.001), and SPA ('yes' significantly distant from 'no', r^2=0.008, p<0.01). Environmental and geographic factors that were found to be significantly correlated with NMDS ordinations (the distances between cells; Table 4.4, Figs. 4.4b,d,f and 4.5b,d,f) were cereals (r^2=0.163, p<0.05), stubbles (r^2=0.248, P<0.01), pastures (r^2=0.188, p<0.05), olives (r^2=0.134, p<0.05), habitat complexity (r^2=0.196, p<0.05) and region (r^2=0.192, p<0.01). GB presence was not significantly correlated with NMDS ordinations at PC scale and at cell scale. When the significant environmental factors were overlaid on species in NMDS visualisation, ordination distances of agro-steppe specialists (Calandra Lark, Short-toed Lark [*Calandrella brachydactyla*] and Little Bustard) and species of conservation concern (Lesser Kestrel, Thekla Lark [*Galerida theklae*] and Red-legged Partridge [*Alectoris rufa*]) from each other were shorter outside of SPAs than inside SPAs.



Figures 4.4a-f: Nonmetric multidimensional scaling (NMDS) ordinations of Bray-Curtis dissimilarity coefficients comparing assemblage composition of point counts (n=955) and 25km^2 cells (n=45). Points represent the placement of point counts or cells within multidimensional space. Categorical environmental factors are colour-coded. (a-b) regions: blue=Central Cáceres, red=Northern Alentejo and Western Badajoz, green=Southern Alentejo,

yellow= Eastern Badajoz (c-d) SPA: green= yes, red= no (e-f) GB presence: blue= yes, orange= no. Region colour-coding corresponds with Figure 4.1. Correlations between ordinations and 'region' and 'SPA' were significant at PC scale (r^2=0.031, p<0.001 and r^2=0.008, p<0.001 respectively). At cell scale, correlation with region was significant (r^2=0.192, p<0.001). Stress of point count plots is 0.18, and of cells 0.17.



Figures 4.5a-f: Nonmetric multidimensional scaling (NMDS) ordinations of Bray-Curtis dissimilarity coefficients comparing assemblage composition of point counts (n= 955) and 25 km^2 cells (n=45). Species locations (in red) represent their placement within multidimensional space. Environmental factors (in blue) that significantly correlate with these ordinations are (a) land-cover types, (b) regions (NAWB is northern Alentejo and southern Badajoz, see Figure 1), and (c) 'SPA yes' or 'SPA no'. Species abbreviations are:

Aler=Red-legged Partridge (*Alectoris rufa*), Calb=Short-toed Lark (*Calandrella brachydactyla*), Cisj=Zitting Cisticola (*Cisticola juncidis*), Cotc=Quail (*Coturnix coturnix*), Embc=Corn Bunting (*Embriza calandra*), Faln=Lesser Kestrel (*Falco naumanni*), Galc=Crested Lark (*Galerida cristata*), Galt=Thekla Lark (*Galerida theklae*), Melc=Calandra Lark (*Melanocorypha calandra*), Saxr=Stonechat (*Saxicola rubicola*), Tett=Little Bustard (*Tetrax tetrax*), Upue=Hoopoe (*Upupa epops*). Stress of point count plots is 0.18, and of cells 0.17.

Table 4.3: Correlations (r^2) of cosine vector of each environmental factor with NMDS ordinations of species assemblages in point counts in Extremadura and Alentejo, April–May 2017. The significance of correlations was computed in envfit function in Oksanen *et al.* (2017). The goodness of fit statistic is the squared correlation coefficient (r^2). Levels of significance are indicated by * <0.05, ** <0.01, *** <0.001.

Environmental factor	***r²***	***p***
Olives	*0.004*	*0.114*
Scrub	*0.002*	*0.446*
Legume	*0.001*	*0.799*
Stubble	*0.012*	*<0.01***
Dry field	*0.006*	*0.04**
Cereals	*0.015*	*<0.001****
Pastures	*0.007*	*0.04**
Ground cover	*0.001*	*0.57*
Habitat complexity	*0.006*	*0.054*
Region (factorial)	*0.031*	*<0.001****
SPA (yes/no)	*0.008*	*<0.001****
Great Bustard presence (yes/no)	*<0.001*	*0.739*

Table 4.4: Correlations (r^2) of cosine vector of each environmental factor with NMDS ordinations of species assemblages in 25 km^2 cells in Extremadura and Alentejo, April–May 2017. The significance of correlations was computed in envfit function in Oksanen *et al.* (2017). The goodness of fit statistic is the squared correlation coefficient (r^2). Levels of significance are indicated by * <0.05, ** <0.01, *** <0.001.

Environmental factor	***r^2***	***p***
Olives	*0.134*	*<0.05**
Scrub	*0.044*	*0.366*
Legume	*0.028*	*0.535*
Stubble	*0.248*	*<0.01***
Dry field	*0.117*	*0.077*
Cereals	*0.163*	*<0.05**
Pastures	*0.188*	*<0.05**
Ground cover	*0.115*	*0.065*
Habitat complexity	*0.196*	*<0.05**
Region (factorial)	*0.192*	*<0.01***
SPA (yes/no)	*0.049*	*0.122*
Great Bustard presence (yes/no)	*0.004*	*0.837*

However, GLM results did not show that abundance was significantly related to SPA in any species (Fig. 4.6). Abundances of Calandra Lark (B(SE)=-1.58(0.80), $p<0.05$) at PC spatial scale), Corn Bunting (-3.16(0.52), $p<0.001$ at PC scale, -0.82(0.33), $p<0.05$ at cell scale), Red-legged Partridge (0.33(0.15), $p<0.05$ at PC scale), Quail (-0.48(0.21), $p<0.05$ at PC scale) and Zitting Cisticola (-1.20(0.33), $p<0.001$ at PC scale) were significantly lower in central Cáceres. Abundance of Little Bustard (0.63(0.28), $p<0.05$ at PC scale) and Lesser Kestrel (3.66(1.33), $p<0.01$ at cell scale) were significantly higher in southern Alentejo. Abundances of Calandra Lark (-3.51(0.81), $p<0.001$) and Short-toed Lark (-1.31(0.43), $p<0.01$) were lower in eastern Badajoz at PC scale, but not at cell scale. Full results of GLMs are in Appendices 4.2.1 and 4.2.2.

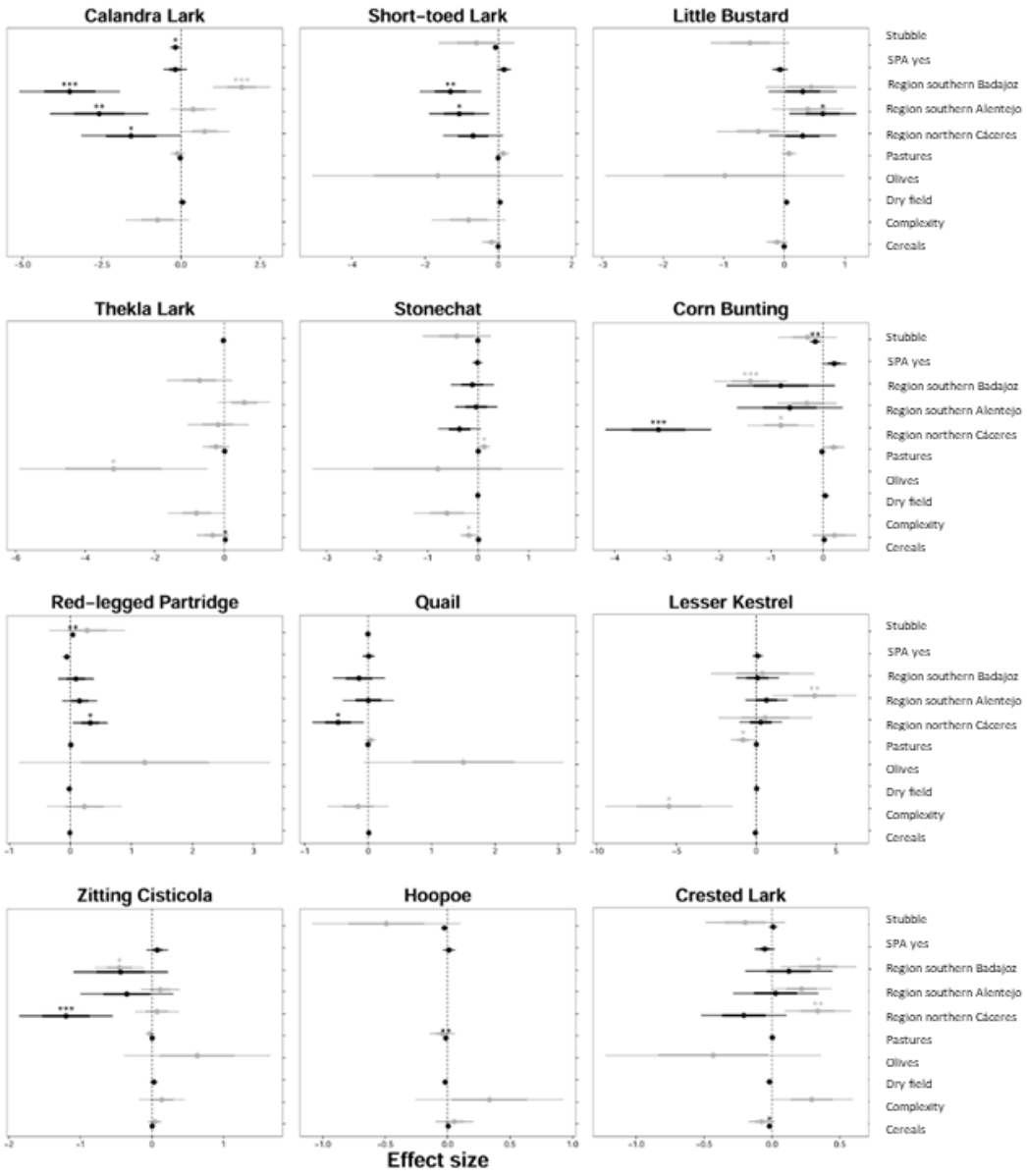


Figure 4.6: Results of generalised linear models relating abundances of breeding farmland species in point counts (black, n=955) and 25 km^2 cells (light grey, n=45) to environmental variables, in Extremadura and Alentejo, April–May 2017. Circles are effect sizes. Thick lines are standard errors. Thin lines are 95% confidence intervals. Significance of variables indicated with '***'= p<0.001, '**'=p<0.01, '*'=p<0.05. Regions (central Cáceres, southern Alentejo, eastern Badajoz), and SPA, are categorical variables.

4.5 Discussion

Great Bustard is potentially a unique example of a surrogate species that may act as an indicator, umbrella and/or flagship species for other steppe species that co-habit agro-steppe systems in southwest Iberia. It is a large species in which both sexes utilise varied habitats during the breeding season, including fallows, cereals, pastures and stubbles (Alonso, Álvarez-Martínez & Palacín 2012; Rocha, Morales & Moreira 2012; Martín *et al.* 2012). However, results of this study indicate that GB is not a good indicator species for all other agro-steppe species in southwest Iberia, especially for species utilising drier habitats: (1) GB numbers did not predict species richness in 25 km^2 cells of any subsets of breeding farmland birds, (2) GB numbers were not correlated with the density of individual farmland-breeding species, apart for Montagu's Harrier, and (3) GB presence was not significantly linked to agro-steppe bird assemblage composition.

Only Montagu's Harrier densities were found to be significantly correlated to GB counts, possibly because both species may benefit locally from similar active conservation measures, such as delay of cereal and hay harvest post fledging, and compensating farmers for their economic loss (Arroyo, Garcia & Bretagnolle 2002; Torres-Orozco *et al.* 2016). The semi-colonial breeding habits of Montagu's Harrier (Arroyo, Mougeot & Bretagnolle 2001; Arroyo, García & Bretagnolle 2004) should be brought into account when evaluating this result. In France, density of breeding Montagu's Harrier was 4.96 ± 0.77 pairs/100 km^2 (Millon *et al.* 2002). At the spatial scale at which correlations between Montagu's Harrier densities and GB numbers were found, 25 km^2 cells, the independence of cells can be assumed. Contrastingly, densities of other species that also breed in tall grass, such as Little Bustard, were

not correlated with GB numbers. It is possible that other, currently unknown, factors may affect the relationship between GB and other breeding farmland species.

This study suggests that wider monitoring programs of agro-steppe and conservation concern species should be established in Extremadura and Alentejo. Current monitoring programs in Extremadura and Alentejo apparently do not provide the scientific basis for analysis of long-term trends apart from Great and Little Bustards (Chapter 2, De Juana 2009). Identification of long-term trends may have important consequences for conservation, by identifying links between land-use changes and bird numbers (see Chapter 3). Identification of the important, best-representative species list for conservation is essential for a sustainable, long-term monitoring program. Niche-based monitoring might be applicable in this system too (Wade *et al.* 2014), possibly focusing also on species of conservation concern that require bare ground and short grass (e.g. Short-toed Lark and Black-bellied Sandgrouse), whose habitat requirements different from Great Bustard. It is also important to consider the possibility that some of the results presented here reflect differences in habitat selection at different spatial scales (Traba *et al.* 2015), and other differences between life histories of species. Further research and analysis are necessary to better understand the exact habitat preferences of different species, during different periods of the annual cycle.

This study represents a snapshot in time, in 2017, and does not account for potential annual variation in densities and abundances of agro-steppe species. Long-term monitoring of additional agro-steppe species may account for annual

variation. However, the study has provided an insight into which environmental factors shape the agro-steppe bird assemblage composition at different spatial scales. Another major limitation of this study is the comparison of GB counts from 2012-2014 with bird counts in 2017. This limitation should be taken into account when considering the results of this study.

The dominance of pastures, stubbles and cereals was shown here to affect both abundances of individual species, and the structure of species assemblages, as implied by overlaying environmental factors on NMDS ordinations both at PC scale and cell scale. Little Bustard, Calandra Lark and Short-toed Lark, all threatened agro-steppe specialists, were more represented in PC dominated by drier land-cover types, pasture and stubble, while generalist farmland species, Crested Lark, Corn Bunting and Zitting Cisticola, were more represented in PC dominated by cereals. Pastures and stubbles are important components of the traditional rotation system (Suárez, Naveso & De Juana 1997; Correal *et al.* 2003), which is currently undergoing a process of intensification (see Chapter 3). Results of this study highlight the importance of pastures and stubbles, as part of cereal and pastoral rotational systems, for agro-steppe specialists and species of conservation concern at the landscape scale.

Additionally, overlaying environmental variables on NMDS ordinations implied that several agro-steppe specialists and species of conservation concern (Little Bustard, Lesser Kestrel, Calandra Lark and Short-toed Lark) were found more in PC outside of SPAs than inside SPAs. Acknowledging the serious limitations of our basic metric to evaluate the level of conservation interventions in SPAs, this study

indicates that at least in some SPAs, land management potentially failed to provide favourable breeding conditions for priority species compared to outside SPAs. Santana *et al.* (2014) showed that in Castro Verde trends of GB, Little Bustard and Lesser Kestrel were more favourable inside the SPA than outside, but for all other farmland breeding bird species groups the reverse was the case. Results from this study, demonstrating that abundances of Little Bustard (at PC scale) and Lesser Kestrel (at cell scale) were higher in southern Alentejo (most cells surveyed were within SPA Castro Verde) compared to other regions, complement the results by Santana *et al.* (2014), suggesting that the effectiveness of SPAs could be enhanced by focusing on a wider range of species, rather than on GB alone.

The composition of PC assemblages in central Cáceres was significantly different from other regions, and several important species' abundances were significantly lower in this region, both at PC scale and cell scale. Abundances of Calandra Lark and Short-toed Lark were significantly lower in eastern Badajoz at PC scale, but were not found to be statistically linked with southern Badajoz at cell scale. This indicates that agro-steppe species are perhaps faring less well in those large regions, and their responses may be scale-dependent. The scale-dependency of links between assemblage composition and environmental factors is also demonstrated by the statistical link found between habitat complexity and assemblage composition at cell scale, but not at PC scale. It is also possible that other environmental and geographical factors, such as climate, latitude, altitude and soil type – which results in different agricultural systems at landscape-scale (i.e. more pastoral systems in poor soils, more arable cultivation in rich soils

(Montserrat & Fillat 1990; Silva, Faria & Catry 2007)) – might contribute to the structure of agro-steppe bird assemblages in this region.

In SPAs in eastern Badajoz, GB were found to have experienced a recent decline (Chapter 2). In SPAs in central Cáceres, recent indications show that GB experience low productivity (Chapter 5). It is possible that agro-steppe SPAs in Extremadura are being degraded and need to be better managed, for GB and for other agro-steppe species as well. There is a need to adopt a regional view of land management policies, SPA management and monitoring, to benefit the agro-steppe bird assemblage across Extremadura and Alentejo.

4.6 Acknowledgments

Special thanks to the two skilled field assistants who shared the fieldwork effort, Re'a Shaish and Daniel Branch. My deep gratitude is to those who supported fieldwork efforts in many ways: Liga para a Protecção da Natureza (LPN) staff in Centro de Educação Ambiental do Vale Gonçalinho (CEAVG), especially Bruno Herlander Martins, Hugo Lousa, Catia Marques, Rita Ramos and Rita Alcazar; Fergus Crystal and Marc Gálvez; Manuel Calderon (ANSER); Martin Kelsey (Birding Extremadura / Casa Rural El Recuerdo); Angel Sánchez and Angel Rodriguez (Junta de Extremadura). Richard Davies, James Gilroy, Valentina Zini and Anderson Saldanha Bueno assisted with analyses in R. Eli Haviv assisted with design of Survey123 app. Swarovski Optik loaned optical equipment used in fieldwork.

4.7 References

Alonso, J.C. (2014) The great bustard: past, present and future of a globally threatened species. *Ornis Hungarica*, **22**, 1–13.

Alonso, J.C., Álvarez-Martínez, J.M. & Palacín, C. (2012) Leks in ground-displaying birds: hotspots or safe places? *Behavioral Ecology*, **23**, 491–501.

Arroyo, B., Garcia, J.T. & Bretagnolle, V. (2002) Conservation of the montagu's harrier (*Circus pygargus*) in agricultural areas. *Animal Conservation*, **5**, 283–290.

Arroyo, B.E., García, J.T. & Bretagnolle, V. (2004*) Circus pygargus* Montagu's Harrier. *BWP Update*, **6**, 41–55.

Arroyo, B., Mougeot, F. & Bretagnolle, V. (2001) Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). *Behavioral Ecology and Sociobiology*, **50**, 109–115.

Bartoń, K. (2013) MuMIn: multi-model inference, R package version 1.9.13. https://CRAN.R-project.org/package=MuMIn.

BirdLife International. (2015) *European Red List of Birds*. Luxembourg.

BirdLife International. (2017a) Species factsheet: *Otis tarda*, http://www.birdlife.org/datazone/

BirdLife International. (2017b) IUCN Red List for Birds, www.birdlife.org

Bivand, R. & Piras, G. (2015) Comparing implementations of estimation methods for spatial econometrics. *Journal of Statistical Software*, **63**, 1–36.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.

Branton, M. & Richardson, J.S. (2011) Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. *Conservation Biology*, **25**, 9–20.

Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (2005) Distance Sampling. *Encyclopedia of Biostatistics*. John Wiley & Sons, Ltd.

Burnham, K.P. & Anderson, R.P. (2004) Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33**, 261–304.

Butler, S.J., Freckleton, R.P., Renwick, A.R. & Norris, K. (2012) An objective, niche-based

approach to indicator species selection. *Methods in Ecology and Evolution*, **3**, 317–326.

Clarke, K.R. & Warwick, R.M. (1994) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory, Plymouth.

Correal, E., Robledo, A., Ríos, S. & Rivera, D. (2003) Mediterranean dryland mixed sheep-cereal systems. *Grassland Science in Europe*, **11**, 2–4.

Dale, V.H. & Beyeler, S.C. (2001) Challenges in the development and use of ecological indicators. *Ecological Indicators*, **1**, 3–10.

De Juana, E. (2009) The dramatic decline of the little bustard *Tetrax tetrax* in Extremadura (Spain). *Ardeola*, ***56***, 119–125.

Delgado, A. & Moreira, F. (2000) Bird assemblages of an Iberian cereal steppe. *Agriculture, Ecosystems & Environment*, **78**, 65–76.

Gao, T., Nielsen, A.B. & Hedblom, M. (2015) Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators*, **57**, 420–434.

Gregory, R.D., van Strien, A., Vorisek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen, R.P.B. & Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 269–288.

Hansson, L. (2000) *Indicators of Biodiversity: Recent Approaches and Some General Suggestions*. Technical report for Swedish Environmental Protection Agency, Stockholm.

Lambeck, R.J. (1997) Focal species: A multi-species umbrella for nature conservation. *Conservation Biology*, **11**, 849–856.

Lane, S. J., Alonso, J. C., & Martín, C. A. (2001). Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? *Journal of Applied Ecology*, **38**, 193–203.

Lopez-Jamar, J., Casas, F., Diaz, M., & Morales, M. B. (2010). Local differences in habitat selection by Great Bustards *Otis tarda* in changing agricultural landscapes: implications for farmland bird conservation. *Bird Conservation International*, **21**, 328–341. doi:10.1017/s0959270910000535

Magaña, M., Alonso, J.C., Martín, C.A., Bautista, L.M. & Martín, B. (2010) Nest-site selection by great bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis*, **152**, 77–89.

Martín, B., Alonso, J.C., Martín, C. A., Palacín, C., Magaña, M. & Alonso, J.A. (2012) Influence of spatial heterogeneity and temporal variability in habitat selection: A case study on a great bustard metapopulation. *Ecological Modelling*, **228**, 39–48.

Miller, D.L. (2017) Distance: distance sampling detection function and abundance estimation. R package version 0.9.7. https://CRAN.R-project.org/package=Distance.

Millon, A., Bourrioux, J.L., Riols, C. & Bretagnolle, V. (2002) Comparative breeding biology of Hen Harrier and Montagu's Harrier: An 8-year study in north-eastern France. *Ibis*, **144**, 94–105.

Montserrat, P. & Fillat, F. (1990) The Systems of Grassland Management in Spain. *Managed Grasslands: regional studies* (ed A. Breymeyer), pp. 37–70. Elsevier B.V., Amsterdam.

Moreno, V., Morales, M. B., & Traba, J. (2010). Avoiding over-implementation of agri-environmental schemes for steppe bird conservation: a species-focused proposal based on expert criteria. *J Environ Manage*, **91**, 1802–1809. doi:10.1016/j.jenvman.2010.03.018

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2017) vegan: Community Ecology Package. R package version 2.4-4. https://cran.r-project.org/package=vegan.

Pakkala, T., Lindén, A., Tiainen, J., Tomppo, E. & Kouki, J. (2014) Indicators of forest biodiversity: Which bird species predict high breeding bird assemblage diversity in boreal forests at multiple spatial scales? *Annales Zoologici Fennici*, **51**, 457–476.

R Core Team. (2017) R: a language and environment for statistical computing, http://www.r-project.org/.

Roberge, J.-M. & Angelstam, P. (2004) Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology*, **18**, 76–85.

Roberge, J.-M. & Angelstam, P. (2006) Indicator species among resident forest birds – A cross-regional evaluation in northern Europe. *Biological Conservation*, **130**, 134–147.

Roberge, J.-M., Mikusiński, G. & Svensson, S. (2008) The white-backed woodpecker: umbrella species for forest conservation planning? *Biodiversity and Conservation*, **17**, 2479–2494.

Rocha, P., Morales, M.B. & Moreira, F. (2012) Nest site habitat selection and nesting performance of the great bustard *Otis tarda* in southern Portugal: implications for conservation. *Bird Conservation International*, **23**, 323–336.

Santana, J., Reino, L., Stoate, C., Borralho, R., Carvalho, C.R., Schindler, S., Moreira, F., Bugalho, M.N., Ribeiro, P.F., Santos, J.L., Vaz, A., Morgado, R., Porto, M. & Beja, P. (2014) Mixed effects of long-term conservation investment in Natura 2000 farmland. *Conservation Letters*, **7**, 467–477.

Schwandner, J., & Langgemach, T. (2011). How much habitat is left for the great bustard (*Otis tarda*)? Human infrastructure and remaining suitable habitat in western Brandenburg (Germany). *Berichte Zum Vogelschutz*, **47**, 193–206.

Siddig, A.A.H., Ellison, A.M., Ochs, A., Villar-Leeman, C. & Lau, M.K. (2016) How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. *Ecological Indicators*, **60**, 223–230.

Silva, J.P., Correia, R., Alonso, H., Martins, R.C., D'Amico, M., Delgado, A., Sampaio, H., Godinho, C. & Moreira, F. (2018) EU protected area network did not prevent a country wide population decline in a threatened grassland bird. *PeerJ*, **6**, e4284.

Silva, J.P., Faria, N. & Catry, T. (2007) Summer habitat selection and abundance of the threatened little bustard in Iberian agricultural landscapes. *Biological Conservation*, **139**, 186–194.

Simberloff, D. (1998) Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? *Biological Conservation*, **83**, 247–257.

Suárez, F., Naveso, M.A. & De Juana, E. (1997) Farming in the drylands of Spain: Birds of the pseudosteppes. *Farming and Birds in Europe. The Common Agricultural Policy and its Implications for Bird Conservation.* (eds D.J. Pain & M.W. Pienkowski), pp. 297–330. Academic Press, San Diego.

Suter, W., Graf, R.F. & Hesst, R. (2002) Capercaillie (*Tetrao urogallus*) and avian biodiversity: Testing the umbrella-species concept. *Conservation Biology*, **16**, 778–788.

Tarjuelo, R., Morales, M.B., Traba, J. & Delgado, M.P. (2014) Are species coexistence areas a good option for conservation management? Applications from fine scale modelling in two steppe birds. *PLoS ONE*, **9**, 1–9.

Torres-Orozco, D., Arroyo, B., Pomarol, M. & Santangeli, A. (2016) From a conservation trap to a conservation solution: Lessons from an intensively managed Montagu's harrier population. *Animal Conservation*, **19**, 436–443.

Traba, J., Morales, M. B., Carmona, C. P., & Delgado, M. P. (2015). Resource partitioning and niche segregation in a steppe bird assemblage. *Community Ecology*, **16**, 178–188.

Veríssimo, D., Fraser, I., Girão, W., Campos, A.A., Smith, R.J. & Macmillan, D.C. (2014) Evaluating conservation flagships and flagship fleets. *Conservation Letters*, **7**, 263–270.

Wade, A.S.I., Barov, B., Burfield, I.J., Gregory, R.D., Norris, K., Vorisek, P., Wu, T. & Butler, S.J. (2014) A niche-based framework to assess current monitoring of European forest birds and guide indicator species' selection. *PLoS ONE*, **9**, e97217.

Appendices

Appendix 4.1: list of agro-steppe breeding species recorded during fieldwork in spring 2017. For each species, information about its incidence in PC or transect (species recorded in transects marked with *), and number of registrations are provided. Additionally, data are provided on which variable was used in DISTANCE to predict its mean density (and standard deviation). 'EX' – species present in Extremadura only. '†' means species of conservation concern in Europe (BirdLife International 2015); 'NT', 'VU' mean IUCN Near Threatened and Vulnerable respectively (BirdLife International, 2017a).

Species	***Incidence (no. of PC / transects)***	***Registrations***	***Detectability formula***	***Mean density (SD) per km²***
Corn Bunting†	*692*	*1792*	*Null*	*53.0(33.8)*
Calandra Lark†	*532*	*4016*	*Null*	*76.9(110.0)*
Zitting Cisticola†	*477*	*1266*	*Null*	*27.0(11.2)*
Little Bustard†NT	*324*	*556*	*Null*	*3.5(2.4)*
Quail†	*276*	*718*	*Null*	*26.5(12.0)*
Crested Lark	*252*	*860*	*Null*	*34.8(16.2)*
Short-toed Lark†	*170*	*846*	*Sward height*	*50.7(43.5)*
Great Bustard†VU	*169*	*234*	*Null*	*2.9(1.6)*
Thekla Lark	*145*	*618*	*Morning / evening*	*43.4(21.6)*
Stonechat†	*130*	*474*	*Null*	*37.1(15.7)*
Lesser Kestrel†	*129*	*399*	*Null*	*15.7(63.0)*
Montagu's Harrier†*	*102*	*129*	*Null*	*2.6(1.1)*
Black-bellied Sandgrouse†*	*99*	*420*	*Morning / evening*	*8.6(13.3)*
Hoopoe	*71*	*144*	*Morning / evening*	*20.7(2.4)*
House Sparrow	*57*	*386*		
*Pin-tailed Sandgrouse*Ex†*	*54*	*191*		
Bee-eater†	*52*	*186*		
Marsh Harrier†*	*46*	*49*		
Spotless Starling	*41*	*119*		
Linnet†	*38*	*132*		
Goldfinch	*28*	*76*		
Stone Curlew†	*25*	*43*		
Spanish Sparrow	*25*	*210*		
Black-winged Kite†*	*24*	*29*		
Tawny Pipit†	*24*	*26*		
White Stork	*20*	*24*		
Iberian Grey Shrike†	*19*	*26*		

Great Spotted Cuckoo	*18*	*24*		
Roller†	*16*	*31*		
Woodchat Shrike†	*14*	*14*		
Raven	*10*	*14*		
Little Owl†	*10*	*10*		
Red-billed Chough†	*9*	*30*		
Black-eared Wheatear†	*9*	*11*		
Melodious Warbler†	*8*	*12*		
Collared Pratincole†	*7*	*32*		
Common Whitethroat	*4*	*4*		
Red-rumped Swallow	*2*	*6*		
Spectacled Warbler†	*1*	*1*		

Appendix 4.2.1: results of average generalised linear models relating abundance of single species to environmental factors, in point counts (n=955): region (factorial, 3 regions, NAWB is reference), SPA (factorial, yes/no, no is reference), stubble, pastures, dry field and cereals. Average models included all models within 2 AICc values of the model with lowest AICc. For each species, mean B(SE) of each variable is provided. Additionally, variables that were found to have significant relationship are in **bold**, with indication of the level of significance: '***'=<0.001, '**'=<0.01, '*'=<0.05. Abbreviation NAWB = northern Alentejo and western Badajoz.

Species	Region northern Cáceres	Region southern Alentejo	Region southern Badajoz	SPA yes	Stubble	Pastures	Dry field	Cereals
Corn Bunting	**-3.16(0.52)*****	-0.64(0.52)	-0.81(0.53)	0.21(0.12)	-0.15(0.05)	-0.02(0.02)	0.04(0.04)	0.02(0.02)
Crested Lark	-0.21(0.16)	0.03(0.16)	0.12(0.16)	-0.05(0.04)	<0.01(<0.01)	0.01(0.02)	-0.02(0.01)	**-0.02(0.01)***
Zitting Cisticola	**-1.20(0.33)*****	-0.35(0.33)	-0.44(0.34)	0.07(0.08)		<0.01(<0.01)	0.03(0.03)	<0.01(<0.01)
Quail	**-0.48(0.26)***	<0.01(0.20)	-0.15(0.21)	0.01(0.05)	-0.01(0.02)	-0.01(0.01)		0.01(0.01)
Short-toed Lark	-0.69(0.42)	**-1.07(0.42)***	**-1.31(0.43)****	0.15(0.10)	-0.07(0.04)	-0.01(0.01)	0.05(0.03)	-0.01(0.02)
Red-legged Partridge	**0.33(0.15)***	0.15(0.14)	0.09(0.15)	-0.06(0.03)	**0.04(0.16)****	0.01(0.01)	-0.02(0.01)	-0.01(0.01)
Thekla Lark					-0.03(0.03)	0.01(0.01)		**0.03(0.01)***
Calandra Lark	**-1.58(0.80)***	**-2.58(0.79)****	**-3.51(0.81)*****	0.18(0.19)	-0.18(0.08)	-0.02(0.02)	0.04(0.06)	
Stonechat	-0.37(0.22)	-0.04(0.21)	-0.11(0.22)	-0.01(0.05)	-0.01(0.02)	<0.01(0.01)	-0.01(0.02)	0.01(0.01)
Hoopoe				0.01(0.02)	-0.03(0.01)	**-0.01(0.01)****	-0.02(0.01)	<0.01(0.01)
Lesser Kestrel	0.29(0.68)	0.65(0.67)	0.08(0.69)	0.09(0.16)		0.01(0.03)	0.03(0.05)	-0.05(0.03)
Little Bustard	0.30(0.28)	**0.63(0.28)***	0.30(0.29)	-0.07(0.07)			0.04(0.02)	-0.01(0.01)

Appendix 4.2.2: results of average generalised linear models relating abundance of single species to environmental factors, in 25 km^2 cells (n=45): region (factorial, 3 regions, NAWB is reference), habitat complexity, stubble, pastures, olives and cereals. Average models included all models within 2 AICc values of the model with lowest AICc. For each species, mean B(SE) of each variable included in the average model are provided. Additionally, variables that were found to have significant relationship are in **bold**, with indication of the level of significance: '***'=<0.001, '**'=<0.01, '*'=<0.05. Abbreviation NAWB = northern Alentejo and western Badajoz.

Species	Region northern Cáceres	Region southern Alentejo	Region southern Badajoz	Habitat complexity	Stubble	Pastures	Olives	Cereals
Corn Bunting	**-0.82(0.33)***	-0.31 (0.29)	**-1.39(0.36)*****		-0.30(0.29)	0.20(0.10)		0.22(0.22)
Crested Lark	**0.34(0.12)****	0.22(0.11)	**0.34(0.14)***	0.29(0.15)	-0.20(0.15)		-0.43(0.41)	-0.08(0.05)
Zitting Cisticola	0.07(0.16)	0.12(0.14)	**-0.46(0.17)***	0.14(0.16)		-0.03(0.03)	0.63(0.52)	0.04(0.05)
Quail				-0.16(0.24)		0.04(0.04)	1.50(0.80)	
Short-toed Lark				-0.81(0.52)	-0.60(0.53)	0.13(0.09)	-1.65(1.75)	-0.18(0.13)
Red-legged Partridge				0.23(0.31)		0.27(0.32)	1.22(1.05)	
Thekla Lark	-0.18(0.45)	0.57(0.38)	-0.71(0.48)	-0.80(0.42)		-0.24(0.20)	**-3.19(1.38)***	-0.34(0.23)
Calandra Lark	0.74(0.40)	0.39(0.37)	**1.91(0.46)*****	-0.74(0.51)				-0.11(0.11)
Stonechat				-0.62(0.34)	-0.43(0.34)	**0.12(0.06)***	-0.80(1.27)	**-0.18(0.09)***
Hoopoe				0.33(0.30)	-0.49(0.30)	-0.04(0.05)		0.05(0.08)
Lesser Kestrel	0.56(1.50)	**3.66(1.33)****	0.40(1.65)	**-5.47(2.03)***		**-0.82(0.39)***		
Little Bustard	-0.43(0.35)	0.39(0.30)	0.44(0.38)		-0.57(0.33)	0.08(0.06)	-0.98(1.00)	-0.12(0.09)

Chapter 5

Decreasing productivity of Great Bustards in their stronghold in Extremadura (Spain) drives a predicted population decline

Photo credit: David Kjaer / Great Bustard Group http://greatbustard.org/

5.1 Abstract

Productivity is one of the four factors that determine population trends. Understanding population trends and what drives them is crucial for the conservation of threatened species. In Extremadura (Spain), the largest concentration of the globally threatened Great Bustard (*Otis tarda*) occurs in a protected area in central Cáceres, 'Zona de Especial Protección para las Aves (ZEPA) Llanos de Cáceres y Sierra de Fuentes', although total spring counts there decreased from 1180 in 2008 to 695 in 2017. Using an exceptional database of spring counts and productivity counts in late summer between 2005 and 2017 in the protected area, it was found that Great Bustard productivity decreased significantly over time. To test if Great Bustard productivity was linked with plant productivity through the study period, Great Bustard productivity rates were correlated with NDVI values through the breeding season, but were not found to be significantly linked. Using spring count data and late summer productivity counts to predict future population outcomes in stage-class matrix population models, it is predicted that numbers of Great Bustards in the study area will drop to under 500 individuals in 10 years, and after 25 years the population would drop below 150 individuals. If productivity rates return to rates similar to those in the mid 2000's, it is predicted that the population would remain stable. Urgent action is needed to clarify the factors that cause these low and decreasing productivity rates, and mitigate these threats to sustain the future of Great Bustards in their core distribution in Extremadura.

5.2 Introduction

Across Europe, farmland species are the fastest declining group of birds (Butler *et al.* 2010). Understanding the demographic processes that lead to declines, or increases in populations, is crucial for the development of management plans (see review in Newton 2004). Demographic processes are determined by four factors: 1) Adult survival 2) Productivity 3) Juvenile survival and 4) Immigration and emigration (Begon, Townsend & Harper 2006). Understanding each one of these components might help to identify the causes, anthropogenic or natural, for demographic changes. This is crucial for the conservation of threatened species (Norris 2004).

In 2010, 57–70% of the global population of the globally Vulnerable Great Bustard (*Otis tarda*) (BirdLife International 2017) were concentrated in Iberia (Alonso & Palacín 2010). In 2014, 6.7–7.6% of the Iberian population were found in Extremadura (Chapter 2). The largest concentration in Extremadura was in central Cáceres, most of which occurred within a protected area, 'Zona de Especial Protección para las Aves (ZEPA) Llanos de Cáceres y Sierra de Fuentes' (Fig. 5.1). Across the study period of 1985 to 2015, Great Bustard numbers there stayed relatively stable between 1985 and 2015, but in recent years indications of a consistent decline in numbers have been noted, with numbers counted in spring dropping from 1,180 in 2008 to 695 in 2017 (Appendix 5.1). The reasons for the apparent decline at ZEPA Llanos de Cáceres y Sierra de Fuentes are unclear, nor are the mechanisms that lead to the correlational link between Great Bustard subpopulation trends and changes in livestock densities, indicated in Chapter 3. This study investigates the links between changes in Great Bustard productivity and changes in plant productivity,

speculating that decreased productivity rates may have contributed to the apparent decline in total numbers counted in spring.

I hypothesize that Great Bustard productivity responds primarily to above-ground plant productivity (ANPP) that is in turn affected by a) weather patterns, and b) livestock grazing during nesting period. The mechanisms in which Great Bustard productivity is linked with ANPP might include the availability of good cover for breeding, affecting nest concealment (Magaña *et al.* 2010), the links between plant productivity and physiological condition of breeding females, influencing the percentage of females breeding, clutch size and viability (suggested by Morales, Alonso & Alonso 2002), and the availability of arthropods, which are necessary food sources for young chicks (Bravo *et al*. 2012; Lane *et al.* 1999; Rocha, Marques, & Moreira 2005) .

Different weather conditions were found to correlate with breeding productivity of Great Bustards in north-west Spain: Winter rainfall was positively correlated with productivity, and spring rainfall was negatively correlated (Morales, Alonso & Alonso 2002). Obviously, ANPP is linked with rainfall. With continuing climate change, reduced winter rainfall and more extreme weather patterns (Acero *et al.* 2017a; b) may relate to Great Bustard productivity in Extremadura as well. Livestock grazing has varying effects on arthropod densities. Livestock grazing was found to decrease grasshopper abundance on cattle rangelands in Montana, USA (O'Neill *et al.* 2003, 2010), spider, bug and beetle numbers on upland grasslands in Scotland (Dennis *et al.* 2008) and Hymenoptera richness and diversity on semi-arid grasslands in Arizona, USA (Debano 2006), all important components of Great Bustard diet (Lane *et al.* 1999; Rocha, Marques & Moreira 2005). Conversely, in Scotland, numbers of arthropods recognised as components of the diet of

moorland birds were affected by grazing treatments differently through time (Dennis *et al*. 2008). A meta-analysis found varying effects of sheep grazing on arthropod populations, including spider abundances that were higher in grazed compared to ungrazed plots (Scohier and Dumont 2012). With increasing livestock densities in southwest Iberian pastoral systems (Chapter 3), Great Bustard nest mortality rates are expected to increase due to higher predation and nest trampling (both are documented causes of Great Bustard nest mortality, Rocha, Morales & Moreira 2012), and chick mortality may increase due to insufficient food supply.

This study first examines the temporal changes in breeding productivity of Great Bustards in ZEPA Llanos de Cáceres y Sierra de Fuentes. Then, this study investigated the link between Great Bustard productivity and ANPP levels. I predicted that Great Bustard productivity and NDVI throughout the breeding season were linked. NDVI is a vegetation growth index that reflects both weather conditions and livestock grazing (Osborne 2006). Further, using contemporary Great Bustard counts, population models were used to predict whether current productivity rates sustain future population trends in ZEPA Llanos de Cáceres y Sierra de Fuentes, and what productivity rates are necessary to predict a stable population.

Results of this study may initiate conservation actions in Spain, and delineate directions for further research on causes and mechanisms of Great Bustard population trends.

5.3 Methods

5.3.1 Bird counts

This study used a time-series of Great Bustard counts from ZEPA Llanos de Cáceres y Sierra de Fuentes between 2005 and 2017 of exceptional quality by a team of professional field ornithologists. Great Bustards were counted in late March (2005 to 2017), when maximum counts of breeding adult males and females are expected (Alonso *et al.* 2005). Productivity counts were carried out in late August / early September each year (2005 to 2016). Late summer counts record females and their offspring, which, following high mortality rates in the incubation and hatching periods (Ena, Martinez & Thomas 1987; Morales, Alonso & Alonso 2002; Rocha, Morales & Moreira 2012), move around in cohorts and can be counted easily (Alonso *et al.* 2005). After August / September, mortality rates drop considerably (Martín *et al.* 2007). Counts were done from a 4X4 vehicle, with frequent stops and scans from vantage points. Each year, the census was carried out over four days, and covered 290 km. Census routes, dates and methodology were repeated precisely each year. In both spring and late summer censuses, coverage of the study area was maximal and included all suitable habitats. Identifiable age classes in spring counts involved yearling males, non-yearling males and females (all ages aggregated). Productivity counts recorded all pulli, without separating them for sex.

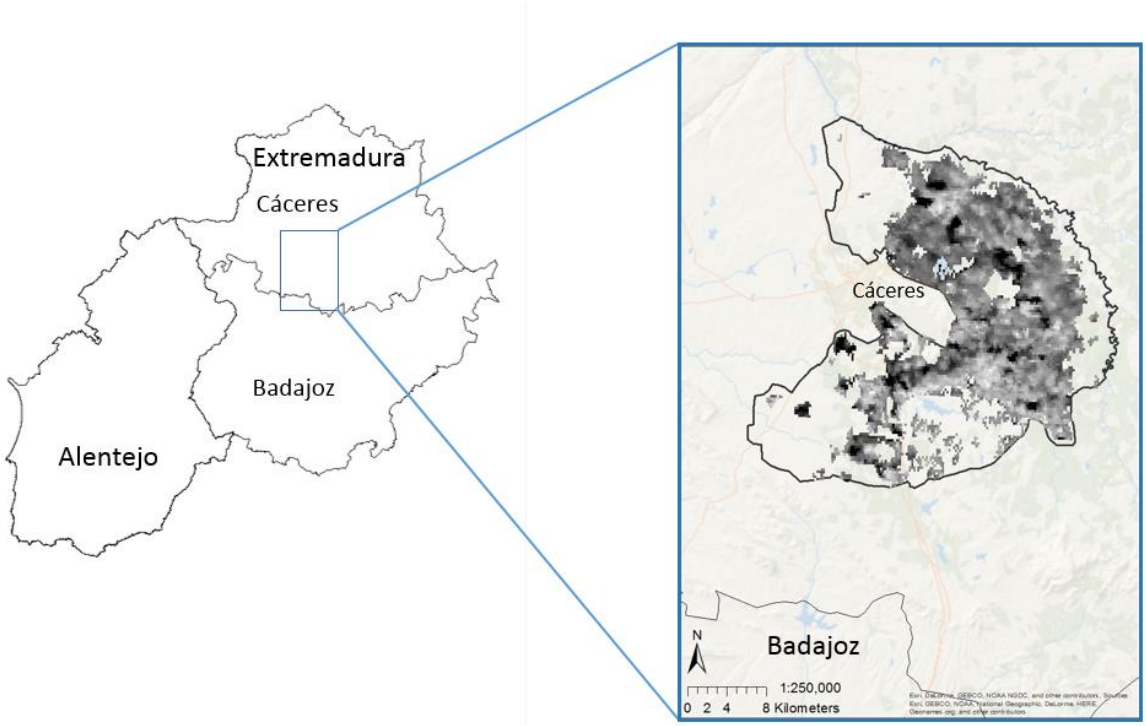


Figure 5.1: Study area (thick black polygon on right map; ZEPA Llanos de Cáceres y Sierra de Fuentes) location in Extremadura (Spain) and Alentejo (Portugal). NDVI values of first half of April 2005 are shown here, in spatial resolution of 250 m.

5.3.2 NDVI

Because plant productivity during the nesting season is affected by complex weather patterns during winter and spring, and explicit livestock data were not available at satisfying spatial resolution, normalised difference vegetation index (NDVI) was used as a proxy for plant productivity. As plant productivity was found to be positively related with arthropod biomass (Perner *et al.* 2005; Pan *et al.* 2017), and NDVI was found to predict arthropod biomass in Arctic tundra (Sweet *et al.* 2015), it may be assumed that also in Iberian agro-steppes NDVI predicts arthropod biomass. NDVI was found to be strongly related to rainfall in Iberia (Immerzeel, Rutten & Droogers 2009) and in a non-montane shrubby semi-arid study system in Uzbekistan (Formica, Burnside & Dolman 2017). NDVI, the difference between the red (RED) and near infrared (NIR) spectral bands, expressed as (NIR - RED)/(NIR + RED), is positively associated with more green vegetation, as leaves absorb the photosynthetically active red band and reflect in the NIR (Osborne 2006).

EROS Moderate Resolution Imaging Spectroradiometer (eMODIS, satellite MYD13Q1) NDVI tiles were used, downloaded from USGS Earth Explorer, at https://earthexplorer.usgs.gov/. This product has 250 m spatial resolution, higher than other leading products (Pettorelli *et al.* 2005; Jenkerson, Maiersperger & Schmidt 2010). NDVI values below zero were excluded from analyses as they likely were non-vegetated areas that do not respond to rainfall (Huete, Justice & van Leeuwen 1999). To compare plant productivity development through the breeding season between years, 16-day composites of three important periods were used: a) for the first half of April, when maximal photosynthetic activity in this region occurs (Osborne, Alonso & Bryant 2001; Osborne 2006) were used. NDVI values at this period across different land-use are likely to represent cover available for breeding female Great Bustards, which depend on pre-harvest cover provided

by cereals, fallow and pastures for breeding (Magaña *et al.* 2010; Rocha, Morales & Moreira 2012); b) for the second half of May, when cereals are cut, but fallows, stubbles and pastures remain uncut; and c) and for the first half of August were used, representing the vegetation condition during the chick-raising period when drying up is extreme. NDVI cell values in each year from 2005 to 2016 were extracted for a layer that included all agro-steppe land-cover types together (identified in Corine Land Cover (Coordination of Information on the Environment Land Cover) 2012; non-irrigated arable land, pastures, fallows and grasslands) in ZEPA Llanos de Cáceres y Sierra de Fuentes (see example if Fig. 5.1), and their means were computed and rescaled at 0.0001 (Didan 2015). NDVI was extracted for all cells, including cells that only intersected with the agro-steppe land-over type layer. Additionally, changes in mean NDVI values between April and May, and between May and August were computed, to represent the differential drying-up process between different land-uses and years. NDVI data were extracted and analysed using R package 'raster' (Hijmans & van Etten 2012).

5.3.3 Data analysis

To test if productivity rates changed through time, Gaussian generalized liner models that related annual near-fledging productivity rates with year and with a quadratic term of year (added to test possible non-linear relationships) were used.

To test if productivity rates were related to NDVI values, I used general linear models that related annual near-fledging productivity rates with annual early April, late May, late August NDVI mean values, and changes between April – May and May – August NDVI mean values.

Near-fledging productivity rates were based on actual productivity counts in this study. Productivity in all analyses was computed as number of near-fledged pulli counted in late summer, divided by the number of adult females in the previous spring. Because of the structure of the count data, in which sexes of pulli, and ages of females and of non-yearling males could not be identified in the field, numbers of those stage classes were estimated. Numbers of adult females were equal to number of all females in spring counts minus estimated numbers of yearling and subadult females. These estimates were based on pulli numbers in previous years, differential yearling mortality rates for males and females, and subadult mortality rates (different mortality rates are in Table 5.2). Females are highly philopatric and their numbers vary as a result of local productivity and mortality only, and immigration is not expected in females (Alonso *et al.* 1998). Therefore, numbers of yearling females and subadult females were computed based on mean actual pulli numbers in three preceding years (in 2005 and 2006 for which there are no data from three preceding years, means were calculated with two nearest years), and sexually-different mortality rates of

yearlings. Numbers of subadult females were the numbers of yearling females in previous year multiplied by the relevant mortality rates.

To generate a prediction what will be the demographic outcome if current productivity rates continue, stage-classified matrix models (Caswell 2001, 2006) were used to predict total numbers of Great Bustards in ZEPA Llanos de Cáceres y Sierra de Fuentes in 30 years (life expectancy of Great Bustard (Alonso *et al.* 2004)), and overall lambda (λ, geometric growth rate: exponent of the slope of linear model relating $\log_{10}$(total number+1) to year), using 1000 permutations. Geometric growth rate was used here even though Great Bustard is a long-lived organism, to provide an intuitive metric for population change. A mean predicted model that averages all 1000 permutations was used to predict the overall end numbers and λ of the population. No carrying capacity was introduced to the models.

Female Great Bustards appear generally to breed first at the age of three years, while males are considered to get their first opportunity to breed at around the age of five (Alonso *et al*. 2004). Therefore, females developed in the models in three stage classes – yearling, subadult (two years old) and adult (three years old or older). Males developed in five stage classes – yearling, subadult1 (two years old), subadult2 (three years old), subadult3 (four years old) and adult (five years old or older). In the model, males and females developed independently, and connected through male pulli produced by breeding adult females, and the necessity of adult males to occur, even in small numbers, in the total population to sustain it. Yearlings and subadults (both males and females) did not remain in the same stage class but either progressed to the next stage class or died. Fecundity occurs only in adult females. Population vectors are in Fig. 5.2; formulae that include stage classes

and demographic parameters in the model matrix are in Table 5.1; rates and data sources of demographic parameters are in Table 5.2.

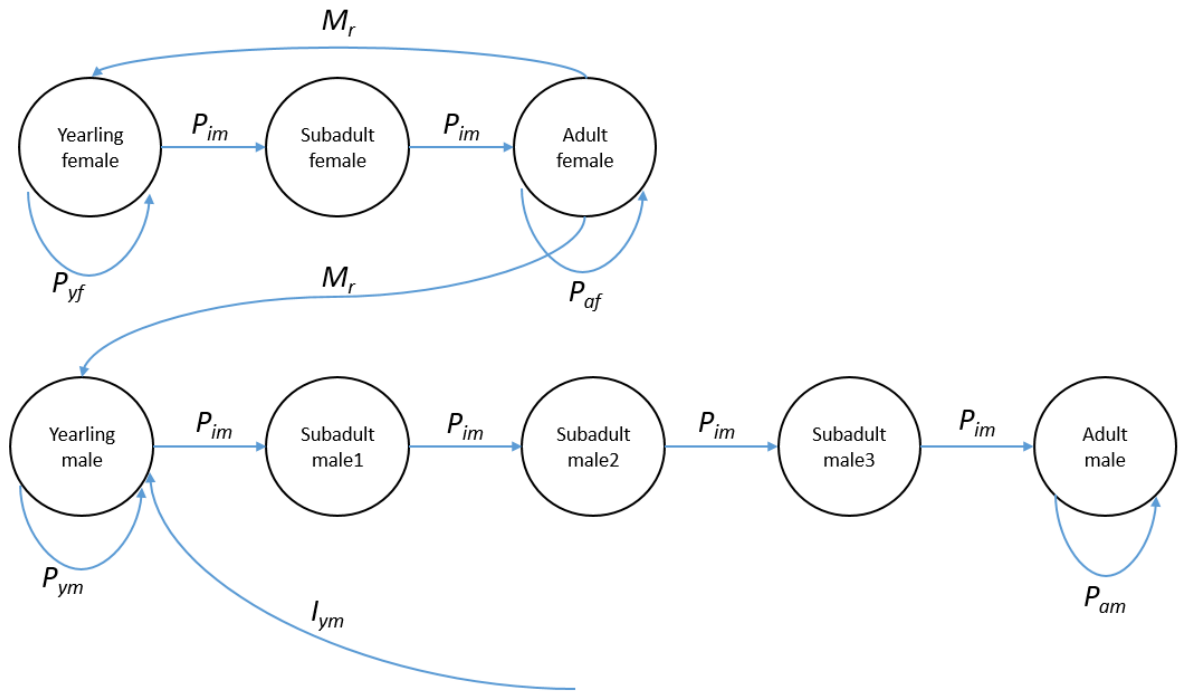


Figure 5.2: Projection vectors of females (top) and males (bottom), describing the population structure used in the matrix models.

Similar to the computation of productivity rates, it was necessary to estimate numbers of some age groups that could not be identified in the field. The method used to calculate the numbers of each age group in Year 1 of the model is elaborated here. Numbers of adult females were equal to number of all females in spring counts minus estimated numbers of yearling and subadult females. These estimates were based on pulli numbers in previous years, differential yearling mortality rates for males and females, and subadult mortality rates. Females are highly philopatric and their numbers are a result of local productivity only (Alonso *et al.* 1998). Therefore, numbers of yearling females and subadult females were computed based on mean actual pulli numbers in the three nearest years (mean of the year, year before and year after, or for 2005 and 2016 year and next two years

or year and two preceding years, respectively), and sexually-different mortality rates of yearlings. Numbers of subadult females were the numbers of yearling females in previous year multiplied by the relevant mortality rates. Numbers of subadult males (three stage classes) were computed based on counts of yearling males and relevant mortality rates. Mortality rates used in these computations were means. However, in the modelling process, stochasticity was introduced through variation in Year 1 start numbers, productivity, mortality and immigration rates (see below).

Table 5.1: Formulae used in population modelling, including definitions of stage classes and demographic parameters. Abbreviations: N_{af} = Adult female (three years old or older) number. N_{saf} = Subadult female (two years old) number. N_{yf} = Yearling female number. N_{am} = Adult male (five years old or older) number. N_{sam3} = subadult3 male (four years old) number. N_{sam2} = Subadult2 male (three years old) number. N_{sam1} = Subadult1 male (two years old) number. N_{ym} = Yearling male number. M_r = productivity rate. P_{af} = adult female mortality rate. P_{am} = adult male mortality rate. P_{im} = immature mortality rates. P_{yf} = yearling female mortality rate. P_{ym}= yearling male mortality rate. I_{ym} = yearling male immigration rate.

Stage class	***Formula***
N_{aft}	$(N_{af\,t-1} * (1-P_{af})) + (N_{saf\,t-1} * (1-P_{im}))$
$N_{saf\,t}$	$N_{yf\ t-1} * (1-P_{im})$
$N_{yf\,t}$	$N_{af\,t-1} * M_r * (1-P_{yf})$
$N_{am\ t}$	$(N_{am\,t-1} * (1-P_{am})) + (N_{sam3\ t-1} * (1-P_{im}))$
$N_{sam3\,t}$	$N_{sam2\,t-1} * (1-P_{im})$
$N_{sam2\,t}$	$N_{sam1\,t-1} * (1-P_{im})$
$N_{sam1\ t}$	$N_{ym\,t-1} * (1-P_{im})$
$N_{ym\ t}$	$N_{af\,t-1} * M_r * (1-P_{ym}) * (1+I_{ym})$

Table 5.2: Demographic parameter estimates and data sources used to construct population models. SD reflects interannual variation in the data used to derive estimates.

Parameter	***Estimate ± SD***	***Source***	***Remarks***
P_{am} - adult male annual mortality	*0.133 ± 0.05*	*Alonso et al. 2004*	*SD from Alonso et al. 2004*
P_{af} - adult female annual mortality	*0.075 ± 0.05*	*Alonso et al. 2004*	*SD from Alonso et al. 2004*
P_{im} – immature annual mortality	*0.133 ± 0.05*	*Alonso et al. 2004*	*No significant difference between mortality rates of immature males and immature females. SD from Alonso et al. 2004*
P_{yf} - yearling female mortality (after August)	*0.546 ± 0.03*	*Martín et al. 2007*	*SD from Martín et al. 2007*
P_{ym} - yearling male mortality (after August)	*0.824 ± 0.06*	*Martín et al. 2007*	*SD from Martín et al. 2007*
I_{ym} - yearling male immigration	*0.96 ± 1.17*	*This study*	*SD from this study*
M_r – annual female productivity	*0.018 ± 0.06*	*This study*	*Per sex. Total productivity is double*

Yearling male numbers counted in spring were higher than expected from local productivity only, implying that inwards immigration from surrounding subpopulations into the study area occurs. Based on other studies, immigration rates of yearling males are significant: in a study in northwestern Spain, 13 yearling males settled in a lek at a mean distance of 18.6 km (±16.0 km) from their natal site (Alonso *et al.* 1998). In this study, only inward immigration of yearling males was assumed to occur, because of the attractiveness of large subpopulations to dispersing yearling males (Martín *et al.* 2008); Great Bustard numbers in ZEPA Llanos de Cáceres y Sierra de Fuentes are the largest in the region (Chapter 2). Immigration is not expected in yearling females that are highly philopatric (Alonso, Morales & Alonso 2000; Morales *et al.* 2000). In the model, immigration rates of yearling males were estimated from counts, assuming that immigration rates differ between years.

Immigration rates were computed using the mean (and SD) difference between expected yearling male numbers based on pulli numbers in previous year and yearling male mortality rates, and observed counts of yearling males.

Other demographic parameters plugged into the model were derived from the literature (primarily Alonso *et al.* (2004); see Table 5.2 for parameter estimates). Sampling variation and inter-annual variation were introduced into the model in several ways. Normally-distributed mortality, reproduction and immigration rates around the mean rate and SD were randomly used as an annual observed estimate in predictions of transfer between each stage class, to imitate environmental stochasticity, truncated at 0 and 1. SD values were derived from literature, reflecting inter-annual variation.

In the matrix model, numbers of all stage classes in Year 1 of the models, used to derive predictions, were based on actual counts and computations of stage class numbers that are unidentifiable in the field (including non-discrete numbers). In the models, Year 1 numbers were randomly selected from a normal distribution derived from the mean count (or derived computation) of each stage class 2015 to 2017 and SD, truncated below 0, imitating variation based on sampling error. Fig. 5.3 shows the matrix model structure, Appendix 5.1 the actual counts in ZEPA Llanos de Cáceres y Sierra de Fuentes 2005 to 2017, and Appendix 5.2 the numbers in Year 1 used in the modelling process.

The use of mean counts from three years to estimate productivity rates and numbers of different stage classes in Year 1 aims to overcome effects of large interannual variation in productivity rates and count numbers (e.g. in 2014, 2015 and 2015 pulli counts were 9, 28 and 20 respectively), while acknowledging the error this introduces to rates and number estimates through the smoothing-out of interannual variation.

♀

$$\begin{bmatrix} P_{yf} & 0 & M_r \\ P_{im} & 0 & 0 \\ 0 & P_{im} & P_{af} \end{bmatrix} \quad \begin{bmatrix} 0.546 & 0 & 0.018 \\ 0.867 & 0 & 0 \\ 0 & 0.867 & 0.925 \end{bmatrix} \quad \begin{bmatrix} 4.31 \\ 3.74 \\ 548.28 \end{bmatrix}$$

♂

$$\begin{bmatrix} I_{ym}+P_{ym} & 0 & 0 & 0 & M_r \\ P_{im} & 0 & 0 & 0 & 0 \\ 0 & P_{im} & 0 & 0 & 0 \\ 0 & 0 & P_{im} & 0 & 0 \\ 0 & 0 & 0 & P_{im} & P_{am} \end{bmatrix} \quad \begin{bmatrix} 0.96+0.176 & 0 & 0 & 0 & 0.018 \\ 0.867 & 0 & 0 & 0 & 0 \\ 0 & 0.867 & 0 & 0 & 0 \\ 0 & 0 & 0.867 & 0 & 0 \\ 0 & 0 & 0 & 0.867 & 0.867 \end{bmatrix} \quad \begin{bmatrix} 29.67 \\ 25.72 \\ 22.30 \\ 19.33 \\ 207.32 \end{bmatrix}$$

Figure 5.3: Matrix models used to predict numbers of Great Bustards. Projection matrices for females (top) and males (bottom) are on the left (formulae) and centre (rates); start numbers are on the right.

An elasticity analysis of the effect of a change of each model parameter on overall λ (geometric growth rate: exponent of the slope of linear model $\log_{10}$(total number) ~ year) was undertaken, following Crowder *et al.* (1994). In the elasticity analysis, each parameter was changed by 10% up and down, and its outcome on all 1000 predicted λ was averaged, to determine a measure of elasticity (E), using: $E = [\lambda_{(x+0.1)} - \lambda_{(x-0.1)}] / [0.2 * \lambda]$, where *x* is the model parameter, weighted against E of other parameter changes to sum up to 1 (Caswell 2001).

All analyses were carried out in R version 1.1.383 (R Core Team 2017). R code used for population modelling is in Appendix 5.3.

5.4 Results

Between 2005 and 2016, Great Bustard productivity decreased from a peak of mean of 87 pulli per 665 adult females in 2005–2008 (0.118 pulli per female), to a low 17.5 pulli per 548 adult females in 2014–2017 (0.035 pulli per female, Fig. 5.2). There was strong support for the model that related productivity with year (ΔAICc= -4.11, Table 5.3), though there was no support found for a non-linear relationship between productivity and year ($F_{1,9}$=9.69, r^2=0.518, p<0.05).

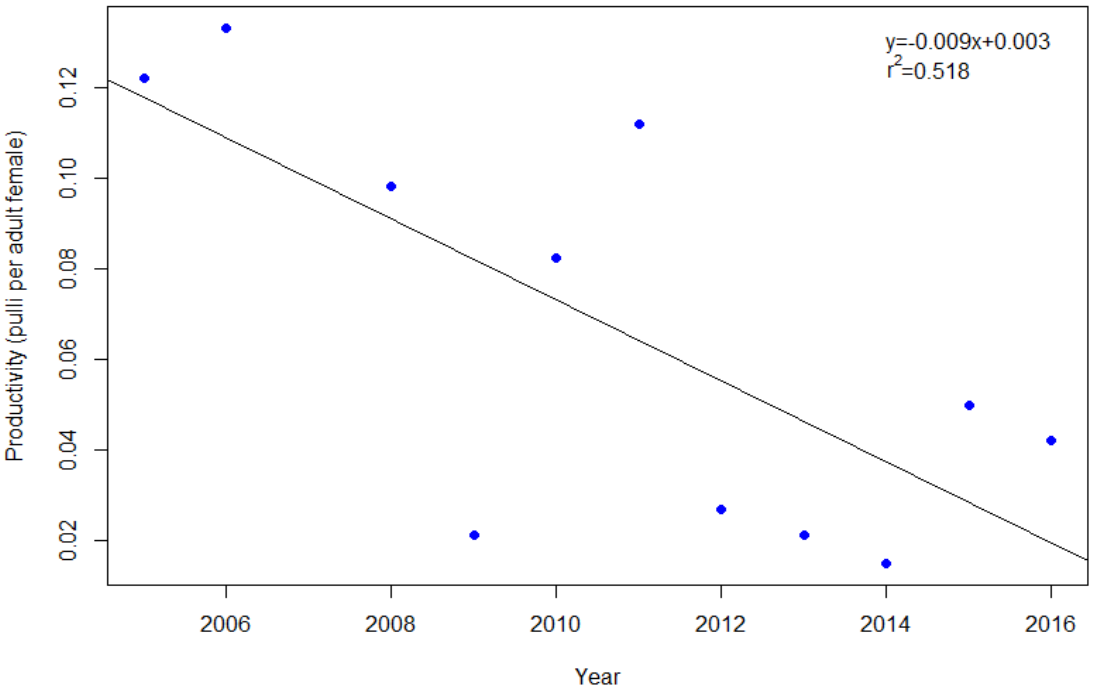


Figure 5.2: Changes in Great Bustard productivity in the study area between 2005 and 2016. Productivity is measured by number of pulli per breeding-age adult female. The black line is the regression line between year and productivity.

Table 5.3: Results of general linear models relating Great Bustard productivity with year and with the quadratic term of year. ΔAICc values are changes in AICc compared to the model with the lowest AICc value. Models are ranked by descending AICc values. **Bold** means support for this model.

Model	***B(SE)***	***df***	***AICc***	***ΔAICc***
Null		*10*	*-32.67*	*0*
Year *Year²*	*-0.020(0.12)* *0.001(0.001)*	*8*	*-32.77*	*-0.10*
Year	***-0.009(0.003)***	***9***	***-36.78***	***-4.11***

There was a strong significant link between NDVI mean values in April and in May (May=0.001*April – 0.22, r^2= 0.47, $F_{1,10}$=10.7, p<0.01), but no significant link was found between NDVI in May and in August (August=0.005*May+0.59, r^2>0.001, $F_{1,10}$=0.004, p=0.953). No statistical link was found between Great Bustard productivity in the study area between 2005 and 2016, and NDVI mean in April ($F_{1,9}$=0.46, r^2=0.049, p=0.51), in May ($F_{1,9}$=1.875, r^2=0.08, p=0.20), and in August ($F_{1,9}$=0.36, r^2=0.038, p=0.561). There was also no statistical link found between Great Bustard productivity in the study area between 2005 and 2016, and NDVI changes between April and May ($F_{1,9}$=1.4, r^2=0.038, p=0.267) and between May and August ($F_{1,9}$=1.58, r^2=0.054, p=0.242).

Based on the population model using mean productivity rates in the years 2014–2016 (11 female pulli and 8 male pulli in Year 1, 0.036 ± 0.018 pulli per female), the mean model predicted that within 10 years the population would drop under 500 individuals, and after 25 years the population would fall below 150 individuals, with an overall λ of 0.919 (Fig. 5.3). If breeding parameters were to improve to mean productivity rates similar to those in 2005–2008 (100 pulli in Year 1, 0.182 ± 0.025 pulli per female) with similar starting

numbers of all other stage classes, the population would remain stable in its numbers throughout the prediction period (Fig. 5.4).

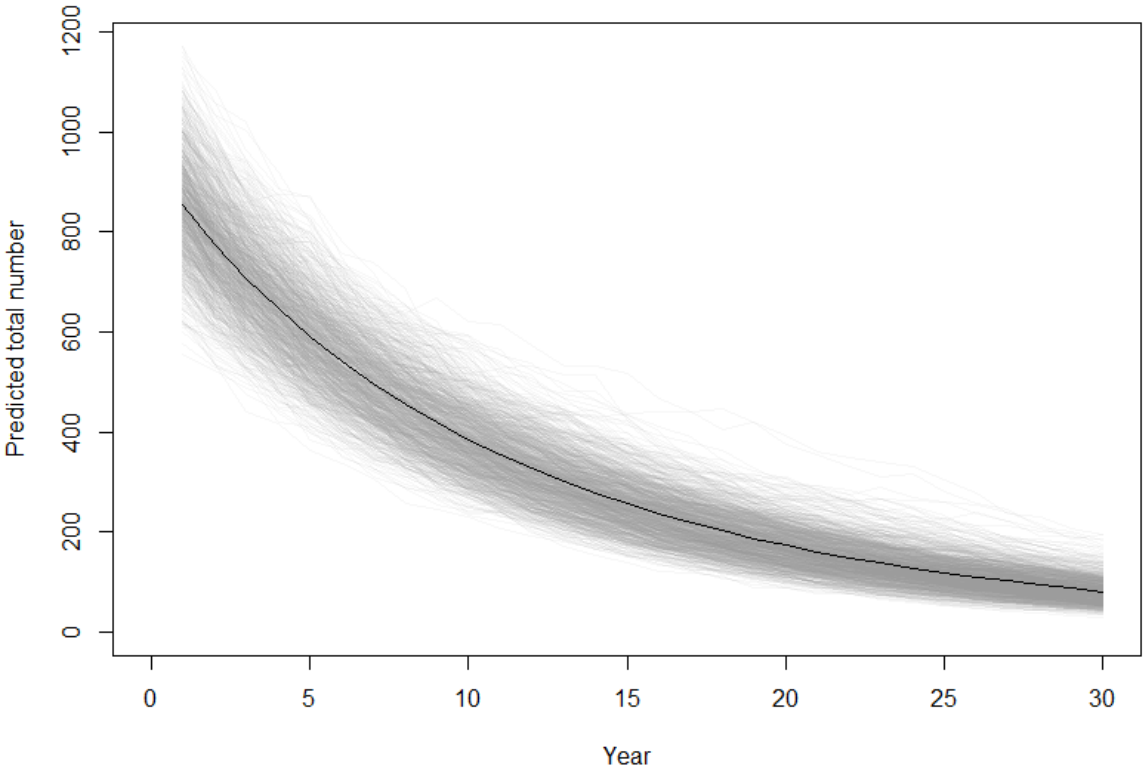


Figure 5.3: Predicted total numbers of Great Bustard in ZEPA Llanos de Cáceres y Sierra de Fuentes in 30 years. Predictions were generated using a population model (1000 permutations), based on actual productivity counts (0.036 ± 0.018 pulli per female, 11 female pulli and 8 male pulli in Year 1) and other demographic parameters taken from the literature. Thin grey lines are individual predictions. The black line is the mean of all 1000 permutations.

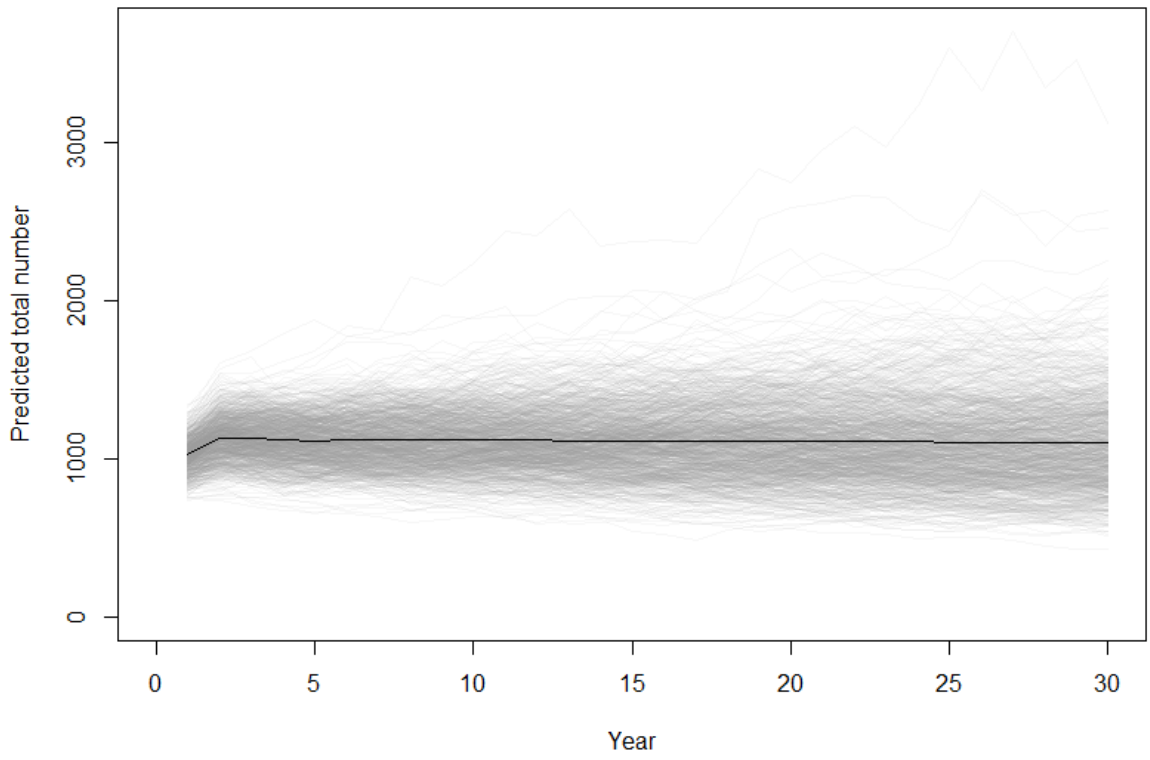


Figure 5.4: Predicted total numbers of Great Bustard in ZEPA Llanos de Cáceres y Sierra de Fuentes in 30 years. Predictions were generated using a population model (1000 permutations), based on productivity rates similar to those in 2005–2008 (0.182 ± 0.025 pulli per female, 100 pulli in Year 1) and other demographic parameters taken from the literature. Thin grey lines are individual predictions. The black line is the mean of all 1000 permutations.

Elasticity analysis showed that overall changes in demographic parameters led to minor changes in λ (Fig. 5.5). Overall population λ in the matrix model was most sensitive to changes in adult female mortality (E=0.47), in yearling male immigration (0.16), and in productivity (0.14) (Fig. 5.6).

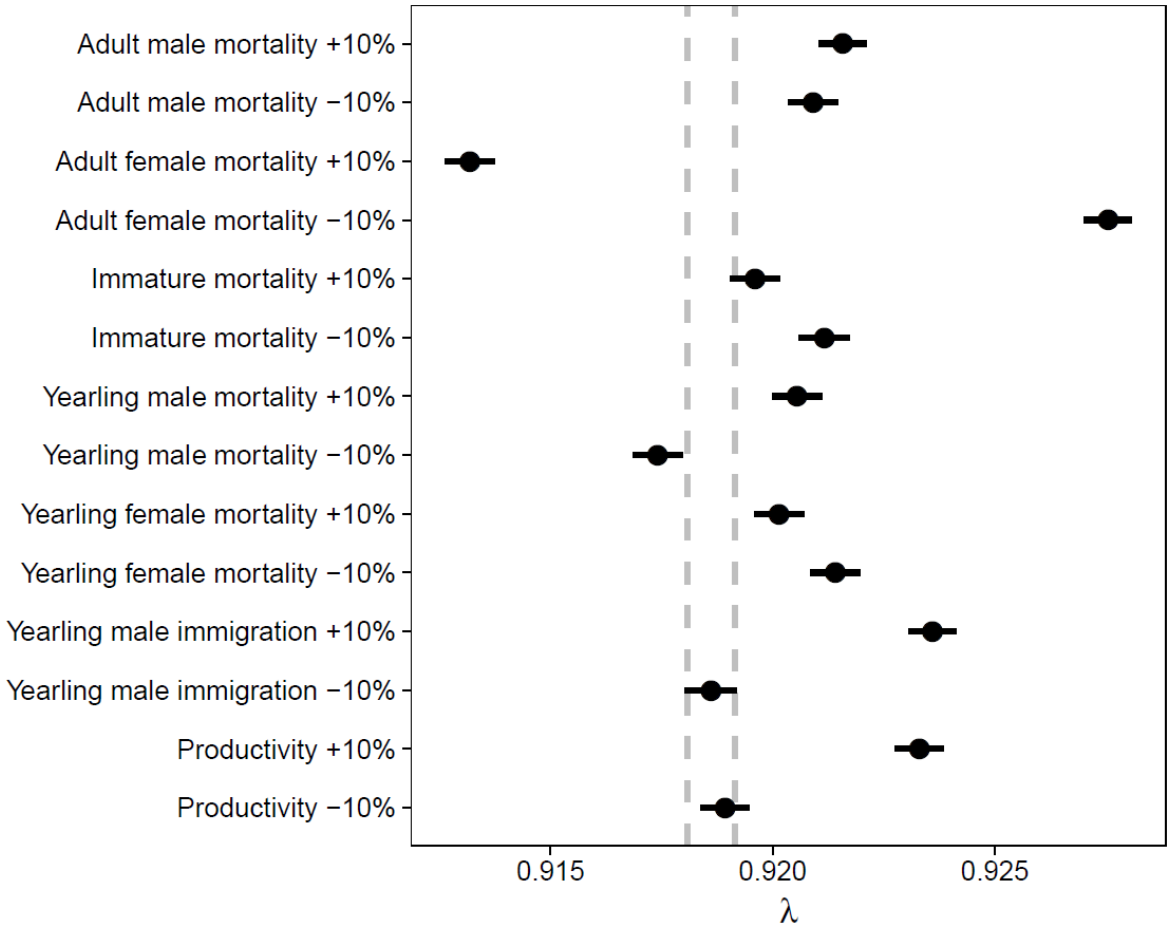


Figure 5.5: Effects of changes in model parameters on overall λ. Black circles are mean λ of all 1000 permutations of models with altered parameters. Black horizontal lines are 95% confidence intervals of those models. Dashed grey vertical lines are 95% confidence intervals of 1000 original, unaltered models.

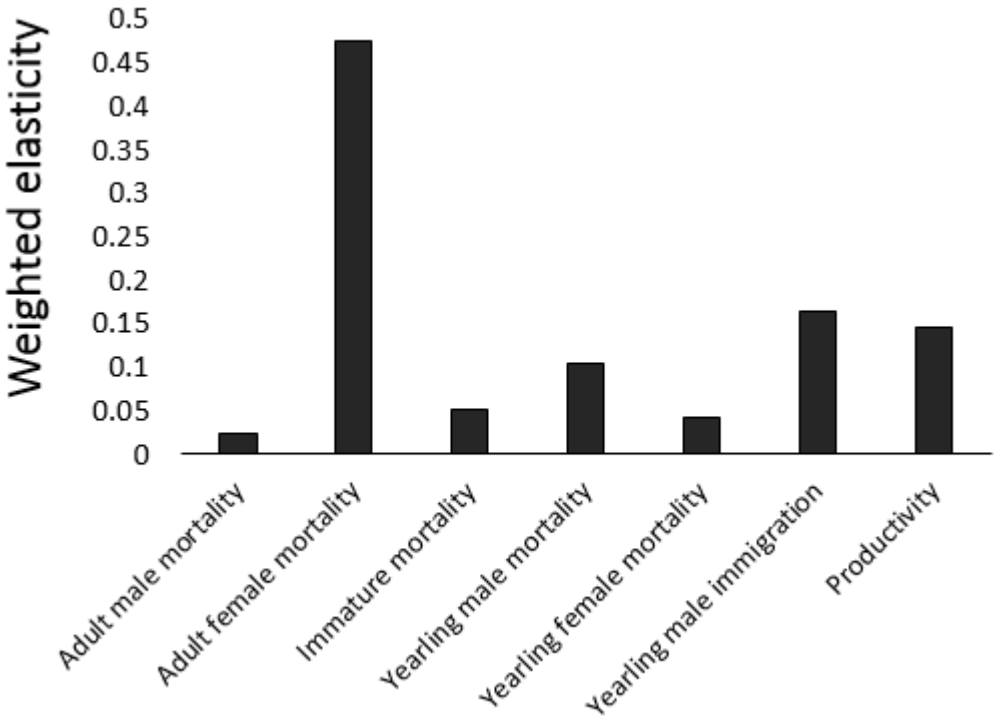


Figure 5.6: Weighted elasticities of model parameters, representing response of overall λ to change of 10% in those parameters.

5.5 Discussion

In its core distribution in Extremadura, the globally Vulnerable Great Bustard (BirdLife International 2017) was found to show alarmingly low productivity rates that have decreased significantly during the study period. These low productivity rates may explain declines in several subpopulations in Extremadura and Alentejo in recent years (see Chapter 2). Current productivity rates in the study area, 0.035 pulli per female, that are much lower than previous published productivity figures from elsewhere in Iberia: mean annual productivity of 0.24 chicks reared per female in central Spain (Martínez 2008), and 0.14 in northwestern Spain (Morales *et al.* 2002).

The reasons for this decline in productivity are, however, unclear. NDVI values through the breeding season that reflect how seasonal vegetation growth is affected by weather and by livestock grazing (Osborne, Alonso & Bryant 2001; Osborne 2006; Formica, Burnside & Dolman 2017) were not found to be statistically linked with Great Bustard near-fledging productivity in this study. In a study on Great Bustard distribution in Spain, only minor differences were found in NDVI between patches occupied and unoccupied by Great Bustards (Osborne, Suarez-Seoane & Alonso 2007). How Great Bustard productivity at local scale is affected by livestock management still needs to be investigated. It is also possible that land-use changes other than changes in livestock densities affected productivity, such as loss of rotational systems (Ribeiro et al. 2014), the abolition of compulsory fallows under 2008 CAP regulations (Matthews 2013) and increases in herbicide use, associated with direct-sown agricultural practices that may have increased in the study region (Juan Traba pers. comm.). The links between Great Bustard productivity and these potential land-use changes were not tested in this study.

Population modelling predicted that current productivity rates may be detrimental to the sustainability of Great Bustards in ZEPA Llanos de Cáceres y Sierra de Fuentes, and perhaps also elsewhere in Extremadura and Alentejo. Sensitivity analysis showed that adult female survival and productivity were most important for population sustainability, in line with other bustard population modelling studies (Alonso *et al.* 2004; Dutta, Rahmani & Jhala 2011; Dolman *et al.* 2015). Yearling male inward immigration was found to impact overall trends too, highlighting the importance of surrounding Great Bustard populations in the region as a source of male settlement in ZEPA Llanos de Cáceres y Sierra de Fuentes.

Population modelling carried out here was based on demographic rates from other parts of Iberia, from the 1990's and early 2000's (Alonso *et al.* 2004; Martín *et al.* 2007). It is possible that, with demographic rates more relevant to Extremadura in current times, results of population models would have been different.

Urgent action needs to be taken, to identify the causes of the current low productivity rates, and to increase these rates to realistic levels that will allow population stability. It is somewhat perplexing to explain such a dramatic change in productivity within ten years, when the entire area is supposed to be managed under an EU-funded Special Protection Area. Perhaps the most important line of investigation should be into the abundance of insects in the chick-rearing period, in case increases in pesticide spraying in surrounding areas have had an impact. Moreover, studies of harvesting practices in these surrounding areas may also reveal an intensification of mechanisation associated with the loss of nests and chicks. Understanding the mechanisms underlying the decrease in productivity may allow their mitigation. Adult mortality rates, especially of females, need to be kept low too, because of their strong influence on overall trends.

5.6 Acknowledgments

Special thanks to Agustín Mogena, Joachim Hellmich and Javier Caldera who obtained, provided and interpreted the data for this study. Thanks to James Gilroy and John Burnside who assisted with NDVI data analysis, and with population modelling. Thanks to Anderson Saldanha Bueno for his assistance in ggploting.

5.7 References

Acero, F.J., Fernández-Fernández, M.I., Carrasco, V.M.S., Parey, S., Hoang, T.T.H., Dacunha-Castelle, D. & García, J.A. (2017a) Changes in heat wave characteristics over Extremadura (SW Spain). *Theoretical and Applied Climatology*, **130**, 1–13.

Acero, F.J., Parey, S., Hoang, T.T.H., Dacunha-Castelle, D., García, J.A. & Gallego, M.C. (2017b) Non-stationary future return levels for extreme rainfall over Extremadura (southwestern Iberian Peninsula). *Hydrological Sciences Journal*, **62**, 1394–1411.

Alonso, J.C. & Alonso, J.A. (1990) *Parámetros Demográficos, Selección de Hábitat Y Distribución de La Avutarda (Otis Tarda) En Tres Regiones Españolas*. ICONA, Madrid.

Alonso, J. C., Martín, E., Alonso, J. A., & Morales, M. B. (1998) Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. *Behavioral Ecology*, **9**, 243–252.

Alonso, J.C., Alonso, J.A., Martín, C.A., Palacín, C., Magaña, M. & Martín, B. (2005) Los censos de avutardas: aspectos metodológicos. *La Avutarda Comun en la Peninsula Iberica: Poblacion Actual y Metodo de Censo* (eds J.C. Alonso, C. Palacín, & C.A. Martín), p. SEO/BirdLife, Madrid.

Alonso, J.C., Martín, C.A., Alonso, J.A., Palacín, C., Magaña, M. & Lane, S.J. (2004) Distribution dynamics of a great bustard metapopulation throughout a decade: Influence of conspecific attraction and recruitment. *Biodiversity and Conservation*, **13**, 1659–1674.

Alonso, J.C., Morales, M.B. & Alonso, J.A. (2000) Partial migration, and lek and nesting area fidelity in female great bustards. *Condor*, **102**, 127–136.

Alonso, J.C. & Palacín, C. (2010) The world status and population trends of the great bustard (*Otis tarda*): 2010 update. *Chinese Birds*, **1**, 141–147.

Alonso, J. A., Martin, C. A., Alonso, J. C., Morales, M. B., & Lane, S. J. (2001). Seasonal movements of male great bustards in central Spain. *Journal of Field Ornithology*, **72**, 504–508.

Alonso, J. C. (2014). The great bustard: past, present and future of a globally threatened species. *Ornis Hungarica*, **22**, 1–13. doi:10.2478/orhu-2014-0014

Alonso, J. C., Álvarez-Martínez, J. M., & Palacín, C. (2012). Leks in ground-displaying birds: hotspots or safe places? *Behavioral Ecology*, **23**, 491–501.

Alonso, J. C., Lane, S. J., Dawson, R., & Idaghdour, Y. (2000). Great bustards *Otis tarda* in Morocco: status in spring 1999 and evidence of a decline in recent decades. *Oryx*, **34**, 141–146.

Alonso, J. C., Magaña, M., Alonso, J. A., Palacín, C., Martín, C. A., & Martín, B. (2009). The most extreme sexual size dimorphism among birds: allometry, selection, and early juvenile development in the great bustard (*Otis tarda*). *Auk*, **126**, 657–665. doi:10.1525/auk.2009.08233

Alonso, J. C., Magaña, M., Palacín, C., & Martín, C. A. (2010). Correlates of male mating success in great bustard leks: the effects of age, weight, and display effort. *Behavioral Ecology and Sociobiology*, **64**, 1589–1600. doi:10.1007/s00265-010-0972-6

Alonso, J. C., Martín, C. A., Palacín, C., Martín, B., & Magaña, M. (2005). The great bustard *Otis tarda* in Andalusia, southern Spain: Status, distribution and trends. *Ardeola*, **52**, 67–78.

Alonso, J. C., Morales, M. B., & Alonso, J. A. (2000). Partial migration, and lek and nesting area fidelity in female great bustards. *Condor*, **102**, 127–136.

Alonso, J. C., & Palacín, C. (2010). The world status and population trends of the great bustard (*Otis tarda*): 2010 update. *Chinese Birds*, **1**, 141–147. doi:10.5122/cbirds.2010.0007

Araújo, M. B., & Rahbek, C. (2012). How does climate change affect biodiversity? *Science*, **313**, 1396–1398. doi:10.1126/science.1131758

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, **29**, 1006–1016. doi:10.1111/cobi.12536

Beketov, M. A., Kefford, B. J., Schäfer, R. B., & Liess, M. (2013). Pesticides reduce regional biodiversity of stream invertebrates. *Proceedings of the National Academy of Sciences*, **110**, 11039–11043. doi:10.1073/pnas.1305618110

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377. doi:10.1111/j.1461-0248.2011.01736.x

Bignal, E. M., & McCracken, D. I. (2000). The nature conservation value of European traditional farming systems. *Environmental Reviews*, **8**, 149–171. doi:10.1139/er-8-3-149

BirdLife International. (2018). Species factsheet: *Otis tarda*. Retrieved from http://www.birdlife.org/datazone/

Blondel, J. (2006). The “design” of Mediterranean landscapes: A millennial story of humans and ecological systems during the historic period. *Human Ecology*, **34**, 713–729.

doi:10.1007/s10745-006-9030-4

Bowen, B. W. (1999). Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. *Molecular Ecology*, **8**, S5–S10. doi:10.1046/j.1365-294X.1999.00798.x

Bravo, C., Ponce, C., Palacín, C., & Carlos Alonso, J. (2012). Diet of young Great Bustards *Otis tarda* in Spain: sexual and seasonal differences. *Bird Study*, **59**, 243–251. doi:10.1080/00063657.2012.662940

Burnside, R. J., Carter, I., Dawes, A., Waters, D., Lock, L., Goriup, P., & Szekely, T. (2012). The UK great bustard *Otis tarda* reintroduction trial: a 5-year progress report. *Oryx*, **46**, 112–121. doi:10.1017/s0030605311000627

Butchart, S. H. M., Scharlemann, J. P. W., Evans, M. I., Quader, S., Aricò, S., Arinaitwe, J., … Woodley, S. (2012). Protecting important sites for biodiversity contributes to meeting global conservation targets. *PLoS ONE*, **7**, 1–8. doi:10.1371/journal.pone.0032529

Butler, S. J., Vickery, J. A., & Norris, K. (2007). Farmland biodiversity and the footprint of agriculture. *Science*, **315**, 111–116.

Caballero, R., Fernández-gonzález, F., Badia, R. P., Molle, G., Roggero, P. P., Bagella, S., … Ispikoudis, I. (2009). Grazing Systems and Biodiversity in Mediterranean Areas: Spain, Italy and Greece. *Pastos*, **39**, 9–152. doi:10.1111/j.1365-2494.2011.00820.x

Calvi, G., Campedelli, T., Tellini Florenzano, G., & Rossi, P. (2018). Evaluating the benefits of agri-environment schemes on farmland bird communities through a common species monitoring programme. A case study in northern Italy. *Agricultural Systems*, **160**, 60–69. doi:10.1016/j.agsy.2017.09.002

Chan, K. M. A., Pringle, R. M., Ranganathan, J., Boggs, C. L., Chan, Y. L., Ehrlich, P. R., … Macmynowski, D. P. (2007). When agendas collide: Human welfare and biological conservation. *Conservation Biology*, **21**, 59–68. doi:10.1111/j.1523-1739.2006.00570.x

Chiron, F., Chargé, R., Julliard, R., Jiguet, F., & Muratet, A. (2014). Pesticide doses, landscape structure and their relative effects on farmland birds. *Agriculture, Ecosystems and Environment*, **185**, 153–160. doi:10.1016/j.agee.2013.12.013

Collar, N., & Garcia, E. F. J. (2018). Great Bustard (*Otis tarda*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions.

Daily, G. C., Polasky, S., Goldstein, J., Kareiva, P. M., Mooney, H. A., Pejchar, L., … Shallenberger, R. (2009). Ecosystem services in decision making: Time to deliver. *Frontiers in Ecology and the Environment*, **7**, 21–28. doi:10.1890/080025

De Frutos, A., Olea, P. P., & Mateo-Tomás, P. (2015). Responses of medium- and large-sized bird diversity to irrigation in dry cereal agroecosystems across spatial scales. *Agriculture, Ecosystems and Environment*, **207**, 141–152. doi:10.1016/j.agee.2015.04.009

De Juana, E. (2009). The dramatic decline of the little bustard *Tetrax tetrax* in Extremadura (Spain). *Ardeola*, **56**, 119–125.

Dennis, P., Skartveit, J., Mccracken, D. I., Pakeman, R. J., Beaton, K., Kunaver, A., & Evans, D. M. (2008). The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology*, **45**, 279–287. https://doi.org/10.1111/j.1365-2664.2007.01378.x

Donald, P. F. (2004). Biodiversity impacts of some agricultural commodity systems. *Conservation Biology*, **18**, 17–37.

Donald, P. F. (2007). Adult sex ratios in wild bird populations. *Ibis*, **149**, 671–692. doi:10.1111/j.1474-919X.2007.00724.x

EEA (2007). Halting the loss of biodiversity by 2010: Proposal for a first set of indicators to monitor progress in Europe. EEA technical report 11/2007.

Faragó, S., Spakovszky, P., & Raab, R. (2014). Conservation of Great Bustard (*Otis tarda*) population of the Mosoni-Plain - a success story. *Ornis Hungarica*, **22**, 14–31. doi:10.2478/orhu-2014-0015

Faria, N., Morales, M. B., & Rabaça, J. E. (2016). Exploring nest destruction and bird mortality in mown Mediterranean dry grasslands: An increasing threat to grassland bird conservation. *European Journal of Wildlife Research*, **62**. doi:10.1007/s10344-016-1039-4

Geiger, F., de Snoo, G. R., Berendse, F., Guerrero, I., Morales, M. B., Oñate, J. J., … Tscharntke, T. (2010). Landscape composition influences farm management effects on farmland birds in winter: A pan-European approach. *Agriculture, Ecosystems & Environment*, **139**, 571–577. doi:10.1016/j.agee.2010.09.018

Giakoumi, S., Hermoso, V., Carvalho, S. B., Markantonatou, V., Dagys, M., Iwamura, T., … Vogiatzakis, I. N. (2018). Conserving European biodiversity across realms. *Conservation Letters*, **11**, e12586. doi:10.1111/conl.12586

Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., … Toulmin, C. (2010). Food security: The challenge of feeding 9 billion people. *Science*, **327**, 812–818. doi:10.1126/science.1185383

Gregory, R. D., van Strien, A., Vorisek, P., Gmelig Meyling, A. W., Noble, D. G., Foppen, R. P. B., & Gibbons, D. W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 269–288. doi:10.1098/rstb.2004.1602

Groves, C. R., Game, E. T., Anderson, M. G., Cross, M., Enquist, C., Ferdaña, Z., … Shafer, S. L. (2012). Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation*, **21**, 1651–1671. doi:10.1007/s10531-012-0269-3

Haines-Young, R. H., & Potschin, M. B. (2010). The links between biodiversity, ecosystem services and human well-being. In D. Raffaelli & C. Frid (Eds.), *Ecosystems Ecology: A New Synthesis*. Cambridge University Press. doi:10.1017/CBO9780511750458

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, **8**, 461–467. doi:10.1111/j.1461-0248.2005.00739.x

Jeliazkov, A., Mimet, A., Chargé, R., Jiguet, F., Devictor, V., & Chiron, F. (2016). Impacts of agricultural intensification on bird communities: New insights from a multi-level and multi-facet approach of biodiversity. *Agriculture, Ecosystems and Environment*, **216**, 9–22. doi:10.1016/j.agee.2015.09.017

Karakaş, R., & Akarsu, F. (2009). Recent status and distribution of the Great Bustard, *Otis tarda*, in Turkey. *Zoology in the Middle East*, **48**, 25–34. doi:10.1080/09397140.2009.10638363

Kessler, A. E., Batbayar, N., Natsagdorj, T., Batsuur', D., & Smith, A. T. (2013). Satellite telemetry reveals long-distance migration in the Asian great bustard *Otis tarda dybowskii*. *Journal of Avian Biology*, **44**, 311–320. doi:10.1111/j.1600-048X.2013.00072.x

Klein Goldewijk, K., Beusen, A., van Drecht, G., & de Vos, M. (2011). The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography*, **20**, 73–86. doi:10.1111/j.1466-8238.2010.00587.x

Lane, S. J., & Alonso, J. C. (2001). Status and extinction probabilities of great bustard (*Otis tarda*) leks in Andalucia, southern Spain. *Biodiversity and Conservation*, **10**, 893–910.

Lane, S. J., Alonso, J. C., & Martín, C. A. (2001). Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? *Journal of Applied Ecology*, **38**, 193–203.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.

Lomba, A., Alves, P., Jongman, R. H. G., & Mccracken, D. I. (2015). Reconciling nature conservation and traditional farming practices: A spatially explicit framework to assess the extent of High Nature Value farmlands in the European countryside. *Ecology and Evolution*, **5**, 1031–1044. doi:10.1002/ece3.1415

Lopez-Jamar, J., Casas, F., Diaz, M., & Morales, M. B. (2010). Local differences in habitat selection by Great Bustards *Otis tarda* in changing agricultural landscapes: implications for farmland bird conservation. *Bird Conservation International*, **21**, 328–341. doi:10.1017/s0959270910000535

Maczulak, A. (2010). *Biodiversity: Conserving Endangered Species*. New York: Facts on File Inc.

Magaña, M., Alonso, J. C., Alonso, J. A., Martín, C. A., Martín, B., & Palacín, C. (2011). Great bustard (*Otis tarda*) nest locations in relation to leks. *Journal of Ornithology*, **152**, 541–548.

Magaña, M., Alonso, J. C., Martín, C. A., Bautista, L. M., & Martín, B. (2010). Nest-site selection by great bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis*, **152**, 77–89.

Martín, C. A., Alonso, J. C., Alonso, J. A., Palacín, C., Magaña, M., & Martín, B. (2007). Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard *Otis tarda*. *Journal of Avian Biology*, **38**, 335–346. doi:10.1111/j.2007.0908-8857.03811.x

Martínez, C. (2008). Distribution, density and productivity of great bustards *Otis tarda* in northwestern Spain: A regional approach. *Journal of Ornithology*, **149**, 507–514.

Matthews, A. (2013). Greening agricultural payments in the EU's Common Agricultural Policy. *Bio-Based and Applied Economics*, **2**, 1–27.

Morales, M. B., Alonso, J. C., & Alonso, J. (2002). Annual productivity and individual female reproductive success in a Great Bustard *Otis tarda* population. *Ibis*, **144**, 293–300.

Morales, M. B., Jiguet, F., & Arroyo, B. (2001). Exploded leks: what bustards can teach us. *Ardeola*, **48**, 85–98.

Moreira, F., Leitão, P. J., Synes, N. W., Alcazar, R., Catry, I., Carrapato, C., … Osborne, P. E. (2012). Population trends in the steppe birds of Castro Verde in the period 2006-2011: consequences of a drought evens and land use changes? *Airo*, **22**, 79–89.

Morgado, R., & Moreira, F. (2000). Seasonal population dynamics, nest site selection, sex-ratio and

clutch size of the great bustard *Otis tarda* in two adjacent lekking areas. *Ardeola*, **47**, 237-246.

Oparin, M. L., Kondratenkov, I. A., & Oparina, O. S. (2003). Abundance of the Transvolga population of great bustard (*Otis tarda* L.). *Biology Bulletin*, **30**, 562–569.

Oparin, M. L., Oparina, O. S., Kondratenkov, I. A., Mamaev, A. B., & Piskunov, V. V. (2013). Factors causing long-term dynamics in the abundance of the Trans-Volga great bustard (*Otis tarda* L.) population. *Biology Bulletin*, **40**, 843–853. doi:10.1134/S1062359013100063

Osborne, P. E., Alonso, J. C., & Bryant, R. G. (2001). Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology*, **38**, 458–471.

Palacín, C., & Alonso, J. C. (2018). Failure of EU Biodiversity Strategy in Mediterranean farmland protected areas. Journal for Nature Conservation, **42**, 62–66. doi:10.1016/j.jnc.2018.02.008

Palacín, C., Alonso, J. C., Alonso, J. A., Magaña, M., & Martín, C. A. (2011). Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard *Otis tarda*. *Journal of Avian Biology*, **42**, 301–308. doi:10.1111/j.1600-048X.2011.05395.x

Palacín, C., Alonso, J. C., Alonso, J. A., Martín, C. A., Magaña, M., & Martin, B. (2009). Differential migration by sex in the great bustard: Possible consequences of an extreme sexual size dimorphism. *Ethology*, **115**, 617–626. doi:10.1111/j.1439-0310.2009.01647.x

Palacín, C., Alonso, J. C., Martín, C. A., & Alonso, J. A. (2016). Changes in bird-migration patterns associated with human-induced mortality. *Conservation Biology*, **31**, 106–115. doi:10.1111/cobi.12758

Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., … Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, **344**, 1090–1092. doi:10.1126/science.1253425

Pinto, M., Rocha, P., & Moreira, F. (2005). Long-term trends in great bustard (*Otis tarda*) populations in Portugal suggest concentration in single high quality area. *Biological Conservation*, **124**, 415–423. doi:10.1016/j.biocon.2005.01.047

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology and Evolution*, **22**, 583–592. doi:10.1016/j.tree.2007.10.001

Raab, R., Julius, E., Greis, L., Schütz, C., Spakovszky, P., Steindl, J., & Schönemann, N. (2014). Endangering factors and their effect on adult Great Bustards (*Otis tarda*) — conservation efforts in the Austrian LIFE and LIFE+ projects. *Aquila*, **121**, 49–63.

Raab, R., Kollar, H. P., Winkler, H., Faragó, S., Spakovszky, P., Chavko, J., … Schütz, C. (2010). Development of the West Pannonian population of the Great Bustard, *Otis tarda* Linnaeus 1758,from 1900 to the winter 2008/2009. *Egretta*, **51**, 74–99.

Rocha, P., Marques, A. T., & Moreira, F. (2005). Seasonal variation in Great Bustard *Otis tarda* diet in south Portugal with a focus on the animal component. *Ardeola*, **52**, 371–376.

Rocha, P., Morales, M. B., & Moreira, F. (2012). Nest site habitat selection and nesting performance of the great bustard *Otis tarda* in southern Portugal: Implications for conservation. *Bird Conservation International*, **23**, 323–336. doi:10.1017/s0959270912000202

Sánchez, A., & Garcia - Baquero, M. J. (2012). La avutarda en Badajoz: Estabilidad, pero con matices. *Quercus*, **314**, 16–22.

Santana, J., Reino, L., Stoate, C., Borralho, R., Carvalho, C. R., Schindler, S., … Beja, P. (2014). Mixed effects of long-term conservation investment in Natura 2000 farmland. *Conservation Letters*, **7**, 467–477. doi:10.1111/conl.12077

Santana, J., Reino, L., Stoate, C., Moreira, F., Ribeiro, P. F., Santos, J. L., … Beja, P. (2017). Combined effects of landscape composition and heterogeneity on farmland avian diversity. *Ecology and Evolution*, **7**, 1212–1223. doi:10.1002/ece3.2693

Schwandner, J., & Langgemach, T. (2011). How much habitat is left for the great bustard (*Otis tarda*)? Human infrastructure and remaining suitable habitat in western Brandenburg (Germany). *Berichte Zum Vogelschutz*, **47**, 193–206.

Scohier, A., & Dumont, B. (2012). How do sheep affect plant communities and arthropod populations in temperate grasslands? *Animal*, **6**, 1129–1138. https://doi.org/10.1017/S1751731111002618

Soulé, M. E. (1985). What is conservation biology? A new synthetic discipline addresses the dynamics and problems of perturbed species, communities, and ecosystems. *BioScience*, **35**, 727–734.

Streich, W. J., Litzbarski, H., Ludwig, B., & Ludwig, S. (2006). What triggers facultative winter migration of Great Bustard (*Otis tarda*) in Central Europe? *European Journal of Wildlife Research*, **52**, 48–53.

Suárez, F., Naveso, M. A., & De Juana, E. (1997). Farming in the drylands of Spain: Birds of the pseudosteppes. In D. J. Pain & M. W. Pienkowski (Eds.), *Farming and Birds in Europe. The Common Agricultural Policy and its Implications for Bird Conservation*. (pp. 297–330). San Diego: Academic Press.

Sunderlin, W. D., Belcher, B., Santoso, L., Angelsen, A., Burgers, P., Nasi, R., & Wunder, S. (2005). Livelihoods, forests, and conservation in developing countries: An overview. *World Development*, **33**, 1383–1402. doi:10.1016/j.worlddev.2004.10.004

Sutcliffe, L. M. E., Batáry, P., Kormann, U., Báldi, A., Dicks, L. V., Herzon, I., … Tscharntke, T. (2015). Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity and Distributions*, **21**, 722–730. doi:10.1111/ddi.12288

Tarjuelo, R., Morales, M., Arroyo, B., Mañosa, S., Bota, G., Casas, F., & Traba, J. (2017). Intraspecific and interspecific competition induces dependent habitat niche shifts in an endangered steppe bird. *Ecology and Evolution*, **7**, 1–11. doi:10.1002/ece3.3444

Tarjuelo, R., Morales, M. B., Traba, J., & Delgado, M. P. (2014). Are species coexistence areas a good option for conservation management? Applications from fine scale modelling in two steppe birds. *Plos One*, **9**, 1–9. doi:10.1371/journal.pone.0087847.g001

Tarjuelo, R., Traba, J., Morales, M. B., & Morris, D. W. (2016). Isodars unveil asymmetric effects on habitat use caused by competition between two endangered species. *Oikos*, **125**. doi:10.1111/oik.03366

Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, **108**, 20260–20264. doi:10.1073/pnas.1116437108

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., … Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, **151**, 53–59. doi:10.1016/j.biocon.2012.01.068

Vadász, C., & Lóránt, M. (2014). Key mortality causes of the Great Bustard (*Otis tarda*) in Central Hungary: An analysis of known fatalities. *Ornis Hungarica*, **22**, 32–41. doi:10.2478/orhu-2014-0016

Van Dyke, F. (2008). *Conservation Biology: Foundations, Concepts, Applications (Second edition)*. Berlin: Springer.

van Strien, A., Pannekoek, J., Hagemeijer, W., & Verstrael, T. (2004). A loglinear poisson regression method to analyse bird monitoring data. *Bird Census News*, **13**, 33–39.

Young, J., Richards, C., Fischer, A., Halada, L., Kull, T., Kuzniar, A., … Watt, A. D. (2007). Conflicts between biodiversity conservation and human activities in the Central and Eastern European countries. *Ambio*, **36**, 545–550. doi:10.1579/0044-7447(2007)36[545:CBBCAH]2.0.CO;2

Appendices

Appendix 5.1: Counts of Great Bustards in ZEPA Llanos de Cáceres y Sierra de Fuentes, incorporating spring counts of adults and yearlings, and productivity counts of pulli in late summer.

Year	***Not-yearling male, spring***	***Yearling male, spring***	***Female, spring***	***Pulli, summer***
2005	*280*	*35*	*582*	*66*
2006	*327*	*5*	*740*	*93*
2007	*N/A*	*N/A*	*N/A*	*116*
2008	*279*	*105*	*786*	*74*
2009	*296*	*75*	*786*	*16*
2010	*351*	*30*	*676*	*54*
2011	*368*	*17*	*602*	*65*
2012	*334*	*56*	*728*	*19*
2013	*344*	*13*	*623*	*13*
2014	*318*	*12*	*613*	*9*
2015	*321*	*8*	*572*	*28*
2016	*185*	*69*	*484*	*20*
2017	*163*	*63*	*469*	*N/A*

Appendix 5.2: Stage classes numbers(SD) in Year 1, used in matrix models. In the 'Realistic' model, numbers are based on counts between 2014 and 2016. In the 'Optimistic' model, yearling female numbers and SD are based on breeding rates in 2005–2007; yearling male numbers and SD are based on yearling male numbers 2008–2010. Subadult numbers and SD were computed using immature mortality rates; adult numbers and SD are similar to 'Realistic' model.

Stage class	***'Realistic' model***	***'Optimistic' model***
Adult female	*548.28(65.91)*	*548.28(65.91)*
Subadult female	*3.74(4.77)*	*18.47(12.51)*
Yearling female	*4.31(4.77)*	*20.81(12.51)*
Adult male	*207.32(77.67)*	*207.32(77.67)*
Subadult3 male	*19.33(5.02)*	*45.62(37.75)*
Subadult2 male	*22.30(5.02)*	*52.62(37.75)*
Subadult1 male	*25.72(5.02)*	*60.69(37.75)*
Yearling male	*29.67(5.02)*	*70(37.75)*

Appendix 5.3: R code for population modelling – realistic model.

```
###define means and SD of demographic rates

admale_mort<- c(0.083,0.133, 0.183)

adfemale_mort<- c(0.025,0.075, 0.125)

imm_mort<- c(0.083,0.133, 0.183)

yearling_male_mort<-  c(0.764, 0.824, 0.884)

yearling_female_mort<-  c(0.543, 0.546, 0.549)

yearling_male_immig<- c(-0.21,0.96,2.13)

pull_prod<- c(0.012, 0.018, 0.024)  #per sex. Total productivity rate is double


##############################################################################################

####create distributions of demographic rates, truncate

##adult male mortality

sd1 <- admale_mort[2]-admale_mort[1]

mn1 <- admale_mort[2]

ad_mort <-rnorm(1000,mn1,sd1)

ad_mort[ad_mort<0]<-0

ad_mort[ad_mort>1]<-1


##adult female mortality

sd2 <- adfemale_mort[2]-adfemale_mort[1]

mn2 <- adfemale_mort[2]

fem_mort <-rnorm(1000,mn2,sd2)

fem_mort[fem_mort<0]<-0

fem_mort[fem_mort>1]<-1
```

```
## imm mortality

sd3 <- imm_mort[2]-imm_mort[1]

mn3 <- imm_mort[2]

im_mor <-rnorm(1000,mn3,sd3)

im_mor[im_mor<0]<-0

im_mor[im_mor>1]<-1


## yearling male immigration

sd4 <- yearling_male_immig[2]-yearling_male_immig[1]

mn4 <- yearling_male_immig[2]

year_imig <-rnorm(1000,mn4,sd4)

year_imig[year_imig<0]<-0

year_imig[year_imig>1]<-1


#yearling female mortality

sd5 <- yearling_female_mort[2]-yearling_female_mort[1]

mn5 <- yearling_female_mort[2]

year_female_mort <-rnorm(1000,mn5,sd5)

year_female_mort[year_female_mort<0]<-0

year_female_mort[year_female_mort>1]<-1


#yearling male mortality

sd6 <- yearling_male_mort[2]-yearling_male_mort[1]

mn6 <- yearling_male_mort[2]
```

```
year_male_mort <-rnorm(1000,mn6,sd6)

year_male_mort[year_male_mort<0]<-0

year_male_mort[year_male_mort>1]<-1



### pulli productivity per female

sd7 <- pull_prod[2]-pull_prod[1]

mn7 <- pull_prod[2]

prod <-rnorm(1000,mn7,sd7)

prod[prod<0]<-0

prod[prod>1]<-1


#####################################################################

###generate first rows for each age class

## ad male

mn8<-207.32

sd8<-77.67

ad_male <- matrix(nrow=30,ncol=1000)

ad_male[1,] <- rnorm(1000,mn8,sd8)

ad_male[ad_male<1]<-1


#subad1_male

mn9<-25.72

sd9<-5.02

subad1_male<-matrix(nrow=30,ncol=1000)
```

```
subad1_male[1,] <- rnorm(1000,mn9,sd9)

subad1_male[subad1_male<0]<-0


#subad2_male

mn10<-22.3

sd10<-5.02

subad2_male<-matrix(nrow=30,ncol=1000)

subad2_male[1,] <- rnorm(1000,mn10,sd10)

subad2_male[subad2_male<0]<-0


#subad3_male

mn11<-19.33

sd11<-5.02

subad3_male<-matrix(nrow=30,ncol=1000)

subad3_male[1,] <- rnorm(1000,mn11,sd11)

subad3_male[subad3_male<0]<-0



##yearling male

mn12<- 29.67

sd12<- 5.02

year_male <- matrix(nrow=30,ncol=1000)

year_male[1,] <- rnorm(1000,mn12,sd12)

year_male[year_male<0]<-0
```

```
## ad female

mn13<- 548.28

sd13<- 65.91

ad_female<- matrix(nrow=30,ncol=1000)

ad_female[1,] <- rnorm(1000,mn13,sd13)

ad_female[ad_female<0]<-0


##yearling female

mn14<- 4.31

sd14<- 4.77

year_female <- matrix(nrow=30,ncol=1000)

year_female[1,] <- rnorm(1000,mn14,sd14)

year_female[year_female<0]<-0



##subad female

mn15<-3.74

sd15<-4.77

subad_female<- matrix(nrow=30,ncol=1000)

subad_female[1,] <- rnorm(1000,mn15,sd15)

subad_female[subad_female<0]<-0


############################################################

###loop for all age classes

for(k in 1:1000){
```

```
  for(i in 2:30){

    ad_female[i,k] <- ad_female[i-1,k]*(1-fem_mort[sample(1:1000,1)])+subad_female[i-1,k]*(1-
im_mor[sample(1:1000,1)])

    ad_male[i,k] <- ad_male[i-1,k]*(1-ad_mort[sample(1:1000,1)])+subad3_male[i-1,k]*(1-
im_mor[sample(1:1000,1)])

    subad3_male[i,k]<- subad2_male[i-1,k]*(1-im_mor[sample(1:1000,1)])

    subad2_male[i,k]<- subad1_male[i-1,k]*(1-im_mor[sample(1:1000,1)])

    subad1_male[i,k]<- year_male[i-1,k]*(1-im_mor[sample(1:1000,1)])

    year_male[i,k] <- ad_female[i-1,k]*prod[sample(1:1000,1)]*(1-
year_male_mort[sample(1:1000,1)])*(1+year_imig[sample(1:1000,1)])

    subad_female[i,k] <- year_female[i-1,k]*(1-im_mor[sample(1:1000,1)])

    year_female[i,k] <- ad_female[i-1,k]*prod[sample(1:1000,1)]*(1-
year_female_mort[sample(1:1000,1)])

  }

}

#########################################################

###calculate totals

totals <- ad_male +
ad_female+year_male+year_female+subad_female+subad1_male+subad2_male+subad3_male
```

Chapter 6

Concluding remarks

6.1 Key findings

This study addressed knowledge gaps about conservation of Great Bustard (*Otis tarda*) and other agro-steppe birds in Extremadura and Alentejo. This study followed a general theme of multi-scales, started from looking at demographic responses at landscape scale, continued to link these demographic responses with land-use changes, then addressed the entire agro-steppe bird assemblage, and finally scrutinized fine-scale mechanisms that might explain demographic responses. The following key evidence is provided in this thesis:

Great Bustard subpopulations experienced variable trends between 1980 and 2014. Negative trends of four subpopulations and positive trends of three subpopulations were significant. Trends of other nine subpopulations were not significant either direction. Overall, large subpopulations remained stable or increased, while small subpopulation decreased, though this difference in trends was not statistically significant. No statistical link was found between subpopulations trends and SPA area. Current counts are much lower than previously published estimates for the region. Since 2010, an alarming decline is noted in most subpopulations (Chapter 2).

Across the study area, the area of habitat types used by breeding GB decreased by 11% between 1990 and 2012, and livestock densities increased between 1989 and 2009 (cattle by 2.7%, sheep by 6.7%). Great Bustard subpopulations trends were not found to be statistically linked with changes in the extent of various land-cover types. However, subpopulation trends were negatively correlationally linked with changes in Livestock Units (Chapter 3).

Great Bustard was not found to be a good surrogate species for agro-steppe bird species. Great Bustard was not found to be a good predictor for richness and densities of

almost all agro-steppe species, apart for Montagu's Harrier (*Circus pygargus*). Great Bustard presence was not significantly statistically linked with agro-steppe assemblage composition. Furthermore, several species of conservation concern were found more outside SPAs than inside SPAs (Chapter 4).

In their stronghold in Extremadura, Great Bustard productivity declined steeply between 2005 and 2016, but was not found to be statistically linked with early April NDVI. If current productivity and other demographic rates continue, this population is predicted to experience a dramatic decline in the next decades (Chapter 5).

6.2 Applications and further research

In this section I will develop the key findings of this study into recommendations for conservation of Great Bustard, other agro-steppe species and their habitats in Extremadura and Alentejo, in hope that these recommendations will be useful for other study species and systems, especially low-intensity agricultural systems. Additionally, I will address the main research priorities that remain unanswered after this study.

6.2.1 Great Bustard monitoring

In the latest assessment of its global conservation status, in 2017, Great Bustard is classified as globally Vulnerable, despite some local increases; preliminary results provided from this study, indicating local decreases in numbers (Chapter 2) and productivity (Chapter 5) contributed to this assessment (BirdLife International 2017b). As a threatened species, Great Bustards are monitored by both relevant government agencies in Extremadura (Junta de Extremadura) and Alentejo (Instituto da Conservação da Natureza e das Florestas, ICNF). This study shows that spring counts of Great Bustards conducted by both agencies are more reliable and consistent in detecting temporal trends than winter counts (Chapter 2). It is important to count Great Bustards frequently, and to improve the quality of counts, e.g. by ensuring the perfect timing of counts in relation to peak lekking period, improving the consistency of count methods across the region, and improving the identification skills of sexes and ages by observers, because of the considerable annual variation in counts of adults, that might occur because of mistiming between counts and peak lekking period. Using long time-series, rather than individual years dotted along the study period, allows modelling that overcomes potential count errors in individual years, to study development of numbers over extended periods (Chapter 2). This methodology is useful for other species

too, and has been used to derive e.g. European bird indices (Gregory *et al.* 2005; PCEBMS 2016).

It is important to identify the appropriate spatial scale to define meaningful demographic units at which changes in numbers of patchily-distributed species represent actual changes in mortality, productivity and immigration rates (Dolman *et al.* 2007; Paradis *et al.* 1999, 2000), affected by internal processes such as land-use changes, and all casual movements are contained within the demographic unit. This study combined information about movements of birds using tracking data from other studies, with statistical analyses examining the spatial scale at which trends explain most variation, to define robust, independent or semi-independent demographic units. In the case of this study they were defined as subpopulations, including those subpopulations stretching across national borders of Extremadura and Alentejo, using 9 km buffers around male locations to indicate potential breeding areas of females (Chapter 2). Acknowledging the methodological limitations of this method (see below), tracking subpopulation trends gives an as-accurate-as-possible picture of Great Bustard population dynamics in the study area. This methodology should become useful to document temporal trends of other species that are monitored regularly and are patchily distributed in the landscape. Similar criteria could be used for other bustard species, which is of considerable conservation value when dealing with transnational populations.

6.2.2 Great Bustard numbers and trends

This study shows that Great Bustards are declining in a globally-important region, Extremadura and Alentejo, with some local variation in subpopulation trends. Across their range in the study area, except for Castro Verde in southern Alentejo, spring counts show a recent from 2010 onwards. Since 2010, numbers of Great Bustards in 13 of the 15 extant subpopulations have dropped considerably (Chapter 2). In ZEPA Llanos de Cáceres y Sierra de Fuentes, the core of Central Cáceres subpopulation, declines in numbers of adults were accompanied by decrease in breeding productivity (Chapter 5), that may be a main driver for these declines in numbers. In long-lived birds, adult mortality rates are often the most important factor in determining the fate of a population, as demonstrated both in field studies and modelling (Dolman *et al.* 2015; Michael *et al.* 2017; Sæther & Bakke 2000; Tuck *et al.* 2001). However, as predicted in Chapter 5, severe declines in productivity rates may lead to population declines also.

The lower estimate provided in this study of the total number of breeding Great Bustards in the study area (about 3,500 birds), lower than previously published estimates (5,500–6,500 birds; Alonso & Palacín 2010; Corbacho *et al.* 2005), requires attention from conservation authorities, in prioritising research of the causes for this decline in one of the strongholds of this species globally. Further research of the links between demographic trends and land-use changes is necessary; clarification of the mechanisms that lead to reduced productivity, and perhaps increase in mortality rates, is important.

6.2.3 Great Bustard conservation

Agricultural intensification in the study area is ongoing (Chapter 3), as traditional agricultural systems are replaced by modern systems. Traditional systems that typically include low-intensity and heterogeneous cereal – pastoral three- or four-year rotational systems are replaced by modern agricultural systems that lose their rotational function, lose their spatial heterogeneity, and increase their intensity by using more irrigation, more permanent crops, more pesticides and higher livestock densities (Cabanillas, Aliseda, & Gallego 2012; Suárez, Naveso, & De Juana 1997). Intensive agricultural practices, in which rotational systems are replaced with permanent cereal and pastoral systems, are becoming more common in the region (Ribeiro *et al*. 2014). Additionally, abolition of compulsory fallows under 2008 CAP regulations may have led to declines in bird species that select fallows for breeding (Matthews 2013). This study showed that the extent of land-cover types that are important for breeding Great Bustards decreased between 1990 and 2012 by 11%, and livestock densities increased between 1989 to 2009 (2.7% increase in cattle, 6.4% in sheep), but land-use databases used in this study were not able to detect such changes. Great Bustard subpopulation trends were found to be negatively statistically related to livestock densities, which is not unexpected, because of the potential adverse effects of high livestock densities on Great Bustard occupancy and breeding. Different bird species show different responses to livestock grazing intensity – some species favour bare ground and select intensively grazed land; other species require tall grass and select lightly grazed land. In Castro Verde, grazing regimes were found to be major drivers of grassland breeding bird densities, with marked variation between different species (Reino *et al.* 2010). In a study in Hungary, grassland species of conservation concern showed contrasting responses to livestock grazing intensity, and Great Bustard showed preference to extensive, lightly-cattle-

grazed pastures (Báldi, Batáry, & Erdos 2005). The mechanism in which livestock grazing may be detrimental to Great Bustard population trends are not fully clear yet. Reduction of cover, necessary for nest safety (Magaña *et al.* 2010), may increase nest predation. Reduction of cover may also reduce available arthropod biomass, important food source for chicks (Lane *et al.* 1999; Rocha, Marques, & Moreira 2005). Breeding conditions for Great Bustards are expected to deteriorate across the region because of (a) increased livestock densities, (b) disturbance increases (Burnside et al., 2014), (c) increase in hay production that is cut early and causes increased nest mortality (Faria, Morales, & Rabaça, 2016a, 2016b), and (d) greater mechanisation and use of fertilisers. In landscapes dominated by heavily-grazed pastures, hay fields may act as ecological traps, attracting females to breed in the only tall-grass crop present in the landscape, and exposing nests to high mortality due to early cutting.

Interestingly, subpopulation trends were not found to be statistically related to changes in the extent of land-cover types, including those that are important for breeding – non-irrigated arable land, pastures and grasslands. It is possible that in scenarios of moderate land-use change, Great Bustards have a limited ability to concentrate in sites that retain good habitat quality. It is also possible that subpopulation trends are driven by other factors, e.g. increases in mortality rates of adults that were not studied here. For several bustard species, infrastructure development in low-intensity agricultural landscapes were identified as main drivers for their decline (Dolman *et al.* 2015; Dutta, Rahmani, & Jhala 2011; Gray *et al.* 2009; Jenkins *et al.* 2011; Mahood *et al*. 2016; Marcelino *et al.* 2017; Santos 2016; Silva *et al.* 2010). Development of infrastructure, mainly powerlines, in the study area may have serious effects on adult mortality rates.

It should be stressed that in sites that undergo dramatic land-use changes, local extirpations may be expected, as reported in Pinto *et al.* (2005). Additionally, several species of conservation concern were found more in sites dominated by pastures and stubbles, both within and outside SPAs (Chapter 4), emphasizing the importance of these land-cover types for conservation of the agro-steppe bird assemblage, not only for Great Bustards.

The sharp decrease in breeding productivity in ZEPA Llanos de Cáceres y Sierra de Fuentes (Chapter 5) is alarming, not only because of its local demographic consequences on the population there, but also because it may reflect what is happening across much of the study area, as agricultural intensification continues across the study area. It is possible that in other fast-declining important subpopulations, such as La Serena, breeding productivity is very low too; this needs to be studied urgently.

To sustain Great Bustard populations in the region, these recommendations may improve the conservation status of Great Bustards and other agro-steppe species:

- Further conversion of sensitive, extensive agro-steppe habitats into intensive land-uses such as permanent crops, irrigated crops and afforestation should be controlled and halted, especially inside SPAs where Great Bustards are concentrated.
- Livestock densities should remain stable or decrease across large spatial scales, with spatial heterogeneity in livestock densities, acknowledging that some priority species for conservation require short grass (Chapter 4).
- Late timing of harvest of cereals and hay is crucial to reduce breeding failure of Great Bustard and other agro-steppe species (Faria, Morales, & Rabaça 2016; Faria, Rabaça, & Morales 2012; Rocha, Morales, & Moreira 2012). Controlling timing of harvest in areas where Great Bustards breed is crucial for their long-term survival.

- These land-management changes could be achieved through implementation of further Agri-Environmental Schemes (AES) that have proven to be especially successful in Castro Verde in increasing numbers of Great Bustards (Pinto *et al.* 2005) and Little Bustards (Chapter 4). More on AES in section 6.2.5.

Within the framework of European agricultural policies that shape the structure of agricultural systems around Europe (Gamero *et al.* 2017; Guerrero *et al.* 2012; Pe'er *et al.* 2014; Ribeiro *et al.* 2014), these tasks are challenging but necessary.

6.2.4 Great Bustard as surrogate for agro-steppe bird species

This study provides several pieces of evidence that demonstrate that Great Bustard is not a perfect surrogate for other agro-steppe bird species in Extremadura and Alentejo (Chapter 4). Great Bustard was not a good predictor for 25 km^2 box species richness; Great Bustard was not a good predictor for density of individual species, except Montagu's Harrier; Great Bustard presence did not shape the structure of the agro-steppe species assemblage.

It is not necessarily accurate to assume that Great Bustard monitoring provides data that indicate the conservation status of other agro-steppe species, especially those of conservation concern. One reason for this may be the interspecific competition shown to take place between Great Bustard and Little Bustard (*Tetrax tetrax*) in Spain at multiple spatial scales (Tarjuelo 2014, 2017, 2016).

Besides Great Bustard, only Little Bustard is monitored regularly in Extremadura and Alentejo, giving insight to its dramatic decline in the study area (De Juana 2009; Silva *et al.* 2018). Other agro-steppe species, including those of conservation concern, are not monitored in any regularity in the study area. To fully understand the conservation status of the entire agro-steppe species assemblage, extension of monitoring efforts to further species will be necessary. Chapter 4 provides ideas for the selection of additional monitored species, including the bare-ground specialists Black-bellied Sandgrouse and Short-toed Larks, and Lesser Kestrel.

This study adds to the general understanding of the selection of surrogate species to indicate the state of the wider biodiversity, by providing information about the ambiguous effectiveness in selection of a large species with complex habitat use to indicate the status of other species sharing different niches in the landscape occupied by the potential

surrogate species. In this study system, Great Bustard is a large, attractive species, and uses multiple land-use types during the breeding period as part of its unique lekking mating system (Alonso, Álvarez-Martínez, & Palacín 2012; Magaña *et al.* 2010; Martín *et al.* 2012). However, it does not perform well as a surrogate for other agro-steppe bird species. It is possible that despite its varied use of different niches by both sexes, Great Bustard breeding takes place only in a specific niche, tall grass or crops, and other agro-steppe species that require different conditions for breeding, e.g. short grass, bare ground or scrub verges, are therefore not well represented by Great Bustard. This result contributes to the knowledge on the selection of surrogate species that should be based on detailed research that links local densities or abundances of supposed surrogate species with those of other species whose conservation status needs to be fully evaluated, based on their niche specificity or generality. It is not safe to assume that a large species that uses multiple habitats during its life cycle would necessarily act as a good surrogate species.

6.2.5 Management and monitoring of protected areas

This study provides several indications that the network of agro-steppe SPAs and SACs that are part of the Natura 2000 network of protected areas in Extremadura and Alentejo may not provide adequate protection for Great Bustard and other priority agro-steppe species. Great Bustard subpopulations trends were not statistically linked with SPA legislation (Chapter 2). It is possible that SPA legislation is not sufficient to ensure favourable habitat management in them, and additional management activities inside SPAs are necessary. Furthermore, abundances of any species were not related to SPA legislation in the point count (Chapter 4). This evidence joins two recent publications that address the function of SPAs in Iberia. Silva *et al.* (2018) showed that population trends of Little Bustards were negative within Portuguese SPAs, although densities were higher than outside SPAs. This result is not wholly consistent with the results of Chapter 4, possibly because Little Bustards were studied at different spatial and temporal scales. Elsewhere in Iberia, Palacín & Alonso (2018) showed that all four species studied (Great and Little Bustards, Montagu's Harrier and Black-bellied Sandgrouse (*Pterocles orientalis*)) showed negative trends in a protected area in central Spain. In a study in SPA Castro Verde, variation in richness and abundance of Great and Little Bustards and Lesser Kestrel between 1995–1997 and 2010–2012 were more favourable inside the SPA than outside, but not favourable for other species assemblages including grassland specialists and species of conservation concern (Santana *et al.* 2014).

All these indications provide a broader picture of the function of the agro-steppe SPAs in Extremadura and Alentejo, and about the function of protected areas in general, and show a diversity of conservation conditions within protected areas. These results raise concerns about the conservation status of agro-steppe birds in these protected areas, implying that legislation alone is not sufficient for the SPA network to provide beneficial

conditions for agro-steppe birds. AES are used widely across Europe as an important tool for better agricultural management of SPAs, especially for farmland birds, in debatable success (Stoate *et al.* 2009, Gamero *et al.* 2017). However, in the study area, effective AES were implemented and/or documented only in Castro Verde, leading to impressive success in increasing Great Bustard numbers there (Pinto *et al.* 2005) as well as benefits for other steppe species (Santana *et al.* 2014). Elsewhere in Extremadura and Alentejo, if AES or other conservation actions were carried out at all, they are local and undocumented. Recent evidence indicates the failure of SPAs to protect target species – Portuguese NATURA 2000 network failed to halt declines of Little Bustards (Silva *et al*. 2018), and four flagship agro-steppe species declined in an SPA in central Spain (Palacín & Alonso 2018). Based on personal observations, it is evident that some local conservation activities were carried out in SPAs, for example fence marking to prevent collision in several subpopulations, provision of water in late summer in ZEPA Llanos de Cáceres y Sierra de Fuentes, nest protection for Montagu's Harriers in La Serena (Manuel Calderon pers. comm.) etc. However, advanced habitat management that includes control of the quality and management of habitats via proactive conservation through AES contracts with farmers has yet to be practised elsewhere in the study area. When AES are competitive economically compared to intensive agriculture (especially in regions with low land costs such as Castro Verde), and lead to advanced habitat management, they can result in impressive success stories, as happened in Castro Verde. This success can be replicated elsewhere in the study area, especially in regions with poor soils and low land costs. This is a major goal for conservation organisations in Extremadura and Alentejo, both governmental and NGO's, to generate interest and allocate sufficient funds to sustain a network of AESs across the study area, that

will actively protect and nurture substantial agro-steppe regions, and enable agro-steppe birds to bounce back from their dire conservation status.

This study also contributes to the effort to evaluate the effectiveness of protected area networks and conservation efforts within them worldwide. Monitoring of wider biodiversity in protected areas is necessary, to ensure that conservation activities, i.e. application of AES in protected areas benefit as many target species as possible (Moreno *et al.* 2010). Using large-scale and long-term data, which systematically compare conservation status inside protected areas and outside them, and across national borders, is a useful tool in conservation. Management of cross-border protected areas is often challenging (Agrawal, 2000; Farhadinia *et al.,* 2015; Kutal *et al*. 2016). Applications of methods used in this study to dilute national borders and adopt a regional approach to conservation may be useful in other study systems too. However, limited information about the conservation activities carried out in protected area confounds the evaluation of the effectiveness of protected areas.

6.2.6 Methodological limitations

This study used several methodologies that necessarily have limitations. First, comparison of Great Bustard counts from early 1980's to counts of modern days is based on assumptions of standardised efforts throughout the period. However, there have been inevitable advances in optics and technology that allowed improvement of the abilities to spot and count birds, identify their sex and age, and accurately record their location. Additionally, through the years, knowledge of the biology of Great Bustards, and their distribution in the study area, has increased, which might have led to increases in the numbers of birds counted during the 1980's (Alonso *et al.* 2005). In this study, these potential biases were minimized by use of counts of adult males as well, not only of total counts, to detect temporal subpopulation trends. Adult males are very large and prominent during the count period, and the chances that they were under-recorded even in the 1980's are lower. Secondly, many of the staff of Junta de Extremadura and ICNF have been taking part in the counts throughout the study period. This gives more confidence in the consistency of count methods between early years and recent years.

The peak lekking period of Great Bustards in spring, at which most females are attracted to and concentrated around lekking males, varies between years (Alonso *et al.* 2005, 2012). Exact timing of counts, in relation to the peak lekking period of Great Bustards, is important in order to reach maximal accuracy in counts. Throughout the study period, count dates were adjusted as much as possible to coincide with peak lekking. However, in a few years, mismatches of a few days between peak lekking and count dates did occur, for various logistical reasons (Angel Sánchez, pers. comm.). This may have led to inaccurate counts, especially of the more secretive females that leave the lek quickly after mating (Magaña *et al.* 2011). Count of adult males are not expected to be affected by a delay of few

days because males do not leave the 'exploded leks' until late April or early May (Alonso, Morales, & Alonso 2000; Morales *et al.* 2000; Morales, Jiguet, & Arroyo 2001). In this study, this potential count error was accounted for by using long time-series in modelling to estimate total numbers, thereby 'smoothing' count errors in specific years. Additionally, the comparison between subpopulation trends of total counts and adult males indicates that if there were any underestimates of female counts, they were minimal.

In two analyses (Chapter 2 and Chapter 4), a simple and limited metric of SPAs was used: whether the relevant area was under SPA legislation or not. Detailed information on what SPA legislation actually translates to on the ground was unavailable at the time of study. Only in Castro Verde was documentation of active conservation activities available. In both chapters, the limitation of this metric for SPA effectiveness is acknowledged, and therefore the results based on the analyses using this metric need to be accepted with attention to this limitation.

In Chapter 4, bird counts were carried out in spring 2017 only. It is clear that local animal densities and abundances may vary between years (e.g. Campbell *et al*. 2015; Nicolaus *et al.* 2016; Moreira *et al.* 2007), possibly because of varying climatic conditions (Moreira *et al.* 2012). In this study, it was not possible to replicate the study efforts in several consecutive years. Still, the study was carried out in a normal climatic year, and the bird densities and abundances recorded are considered here to represent well the conservation status of agro-steppe species assemblage. This limitation is acknowledged in the chapter.

In Chapter 5, population modelling is used to predict the fate of the Great Bustard population in ZEPA Llanos de Cáceres y Sierra de Fuentes. First, several demographic

parameters used in the modelling process were estimated based on studies from elsewhere in Iberia, in the 1990's and early 2000's (Alonso *et al.* 2004; Martín *et al.* 2007, 2008). Using these estimates might have led to errors in modelling. This uncertainty about demographic parameters needs to be acknowledged when discussing the results presented in Chapter 5 regarding the dramatic decline predicted in the population there. Further, Caswell (2001) phrased nicely that 'population modelling is equivalent to driving at 60 km/h', implying that modelling predicts the future but does not guarantee that the prediction will actually fulfil itself. These are the results of the population modelling that predict a negative outcome for the population if current demographic rates do not change. However, population modelling predictions need to be taken with the necessary caution, aiming to minimize uncertainty in demographic parameters to make predictions more robust.

6.2.7 Further research priorities

Analysis of temporal trends of Great Bustard subpopulations in Chapter 2 was based on tracking data available from the 1990's and early 2000's, mainly from other parts of Iberia (e.g. Alonso *et al.* 2004; Alonso *et al.* 1998; Martín *et al.* 2007, 2008). Validating the assumptions upon which the spatial definitions of subpopulations were defined using up-to-date tracking data of birds from the study area would allow more confidence in the methodology used.

Great Bustard counts used in Chapter 2 were up-to-date until 2014 (Alentejo) and 2015 (Extremadura). Completing the time series until 2018 would allow further tracking of the decline across the study area noted in Chapter 2.

Infrastructure development is a cause for population-level changes in other bustards (Jenkins *et al.* 2011; Mahood *et al.* 2016) and a major cause of mortality of Little Bustards in the study area (Marcelino *et al.* 2017; Silva *et al.* 2010). Understanding how long-term Great Bustard subpopulations trends are linked with infrastructure development may provide an important insight on why some subpopulations are declining. At the time of this study on Chapter 3, data on powerline transmission lines was not readily available for Extremadura. If those data do become available, interesting research opportunities might open up.

The study in Chapter 4 did provide evidence that Great Bustard is not a good surrogate for all agro-steppe species, but did not provide direct suggestions which species should be selected for monitoring to represent the entire agro-steppe assemblage. Further research could use the same data to develop more advanced monitoring indices. One option is to follow the niche-based framework (Wade *et al.* 2014) and define indicators based on their niche-use in the landscape.

Detailed livestock data were not available when analysing changes in Great Bustard breeding productivity in ZEPA Llanos de Cáceres y Sierra de Fuentes in Chapter 5. If livestock data and productivity data are available other regions (for example the well-studied Great Bustard population in Castro Verde), it may be possible to statistically link changes in productivity, similar to those reported in Chapter 5 with changes in livestock densities or in livestock types (e.g. sheep vs. cattle).

Furthermore, it might be possible to carry out experimental productivity studies, in which productivity of Great Bustards in large fenced parcels of pasture excluded from grazing in a heavily grazed landscape (e.g. Brozas in Cáceres) would be compared with control plots with grazing.

6.3 References

Agrawal, A. (2000). Adaptive management in transboundary protected areas: The Bialowieza National Park and Biosphere Reserve as a case study. *Environmental Conservation*, **27**, 326–333.

Alonso, J. C., Alonso, J. A., Martín, C. A., Palacín, C., Magaña, M., & Martín, B. (2005). Los censos de avutardas: Aspectos metodológicos. In J. C. Alonso, C. Palacín, & C. A. Martín (Eds.), *La Avutarda Comun en la Peninsula Iberica: Poblacion Actual y Metodo de Censo*. Madrid: SEO/BirdLife.

Alonso, J. C., Álvarez-Martínez, J. M., & Palacín, C. (2012). Leks in ground-displaying birds: hotspots or safe places? *Behavioral Ecology*, **23**, 491–501.

Alonso, J. C., Martín, C. A., Alonso, J. A., Palacín, C., Magaña, M., & Lane, S. J. (2004). Distribution dynamics of a great bustard metapopulation throughout a decade: influence of conspecific attraction and recruitment. *Biodiversity and Conservation*, **13**, 1659–1674.

Alonso, J. C., Martín, E., Alonso, J. A., & Morales, M. B. (1998). Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. *Behavioral Ecology*, **9**, 243–252.

Alonso, J. C., Morales, M. B., & Alonso, J. A. (2000). Partial migration, and lek and nesting area fidelity in female great bustards. *Condor*, **102**, 127–136.

Alonso, J. C., & Palacín, C. (2010). The world status and population trends of the great bustard (*Otis tarda*): 2010 update. *Chinese Birds*, **1**, 141–147. doi:10.5122/cbirds.2010.0007

Báldi, A., Batáry, P., & Erdos, S. (2005). Effects of grazing intensity on bird assemblages and populations of Hungarian grasslands. *Agriculture, Ecosystems and Environment*, **108**, 251–263. doi:10.1016/j.agee.2005.02.006

BirdLife International. (2017a). IUCN Red List for Birds. Retrieved December 14, 2017, from http://www.birdlife.org/datazone/

BirdLife International. (2017b). Species factsheet: *Otis tarda*. Retrieved December 14, 2017, from http://www.birdlife.org/datazone/

Burnside, R. J., Végvári, Z., James, R., Konyhás, S., Kovács, G., & Székely, T. (2014). Human disturbance and conspecifics influence display site selection by great bustards *Otis tarda*. *Bird Conservation International*, ***24***, 32–44. doi:10.1017/s0959270913000142

Cabanillas, F. J. J., Aliseda, J. M., & Gallego, J. A. G. (2012). Land cover and land use change in the

central Spanish-Portuguese border region. *Boletín de La Asociación de Geógrafos Españoles*, *60*, 369–398.

Campbell, G. S., Thomas, L., Whitaker, K., Douglas, A. B., Calambokidis, J., & Hildebrand, J. A. (2015). Inter-annual and seasonal trends in cetacean distribution, density and abundance off southern California. *Deep-Sea Research Part II: Topical Studies in Oceanography*, **112**, 143–157. doi:10.1016/j.dsr2.2014.10.008

Caswell, H. (2001). *Matrix population modelling* (2nd ed.). Sunderland, MA, USA: Sinauer Associates.

Corbacho, C., Fernández, E., Costillo, E., Lozano, A., & Gil, A. (2005). La avutarda común en Extremadura: distribución, población y tendencias. In J. C. Alonso, C. Palacín, & C. A. Martín (Eds.), *La Avutarda Comun en la Peninsula Iberica: Poblacion Actual y Metodo de Censo* (pp. 44–63). Madrid: SEO/BirdLife.

De Juana, E. (2009). The dramatic decline of the Little Bustard *Tetrax tetrax* in Extremadura (Spain). *Ardeola*, **56**, 119–125.

Dolman, P. M., Collar, N. J., Scotland, K. M., & Burnside, R. J. (2015). Ark or park: The need to predict relative effectiveness of ex situ and in situ conservation before attempting captive breeding. *Journal of Applied Ecology*, **52**, 841–850. doi:10.1111/1365-2664.12449

Dolman, P. M., Hinsley, S. A., Bellamy, P. E., & Watts, K. K. (2007). Woodland birds in patchy landscapes: The evidence base for strategic networks. *Ibis*, **149**, 146–160. doi:10.1111/j.1474-919X.2007.00748.x

Dutta, S., Rahmani, A. R., & Jhala, Y. V. (2011). Running out of time? The great Indian bustard *Ardeotis nigriceps* - status, viability, and conservation strategies. *European Journal of Wildlife Research*, **57**, 615–625. doi:10.1007/s10344-010-0472-z

Farhadinia, M. S., Ahmadi, M., Sharbafi, E., Khosravi, S., Alinezhad, H., & Macdonald, D. W. (2015). Leveraging trans-boundary conservation partnerships: Persistence of Persian leopard (*Panthera pardus saxicolor*) in the Iranian Caucasus. *Biological Conservation*, **191**, 770–778. doi:10.1016/j.biocon.2015.08.027

Faria, N., Morales, M. B., & Rabaça, J. E. (2016). Exploring nest destruction and bird mortality in mown Mediterranean dry grasslands: An increasing threat to grassland bird conservation. *European Journal of Wildlife Research*, **62**. doi:10.1007/s10344-016-1039-4

Faria, N., Rabaça, J. E., & Morales, M. B. (2012). The importance of grazing regime in the provision of breeding habitat for grassland birds: The case of the endangered little bustard (*Tetrax tetrax*).

Journal for Nature Conservation, **20**, 211–218. doi:10.1016/j.jnc.2012.03.003

Gamero, A., Brotons, L., Brunner, A., Foppen, R., Fornasari, L., Gregory, R. D., … Voříšek, P. (2017). Tracking progress toward EU biodiversity strategy targets: EU policy effects in preserving its common farmland birds. *Conservation Letters*, **10**, 394–401. doi:10.1111/conl.12292

Gray, N. T. E., Chamnan, H., Collar, N. J., & Dolman, P. M. (2009). Sex-specific habitat use by a lekking bustard: conservation implications for the critically endangered bengal florican (*Houbaropsis bengalensis*) in an intensifying agroecosystem. *The Auk*, **126**, 112–122.

Gregory, R. D., van Strien, A., Vorisek, P., Gmelig Meyling, A. W., Noble, D. G., Foppen, R. P. B., & Gibbons, D. W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 269–288. doi:10.1098/rstb.2004.1602

Guerrero, I., Morales, M. B., Oñate, J. J., Geiger, F., Berendse, F., Snoo, G. de, … Tscharntke, T. (2012). Response of ground-nesting farmland birds to agricultural intensification across Europe: Landscape and field level management factors. *Biological Conservation*, **152**, 74–80. doi:10.1016/j.biocon.2012.04.001

Jenkins, A. R., Shaw, J. M., Smallie, J. J., Gibbons, B., Visagie, R., & Ryan, P. G. (2011). Estimating the impacts of power line collisions on ludwig's bustards *Neotis ludwigii*. *Bird Conservation International*, **21**, 303–310. doi:10.1017/S0959270911000128

Kutal, M., Váňa, M., Suchomel, J., Chapron, G., & López-Bao, J. V. (2016). Trans-Boundary edge effects in the western carpathians: The influence of hunting on large carnivore occupancy. *PLoS ONE*, **11**, 1–15. doi:10.1371/journal.pone.0168292

Lane, S. J., Alonso, J. C., Alonso, J. A., & Naveso, M. A. (1999). Seasonal changes in diet and diet selection of great bustards (*Otis t. tarda*) in north-west Spain. *Journal of Zoology*, **247**, 201–214.

Magaña, M., Alonso, J. C., Alonso, J. A., Martín, C. A., Martín, B., & Palacín, C. (2011). Great bustard (*Otis tarda*) nest locations in relation to leks. *Journal of Ornithology*, **152**, 541–548.

Magaña, M., Alonso, J. C., Martín, C. A., Bautista, L. M., & Martín, B. (2010). Nest-site selection by great bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis*, **152**, 77–89.

Mahood, S. P., Silva, J. P., Dolman, P. M., & Burnside, R. J. (2016). Proposed power transmission lines in Cambodia constitute a significant new threat to the largest population of the Critically Endangered Bengal florican *Houbaropsis bengalensis*. *Oryx*, **50**, 1–9. doi:10.1017/S0030605316000739

Matthews, A. (2013). Greening agricultural payments in the EU's Common Agricultural Policy. *Bio-Based and Applied Economics*, **2,** 1–27.

Marcelino, J., Moreira, F., Mañosa, S., Cuscó, F., Morales, M. B., García de la Morena, E. L., … Silva, J. P. (2017). Tracking data of the little bustard (*Tetrax tetrax*) in Iberia shows high anthropogenic mortality. *Bird Conservation International*, **27**. doi:10.1017/S095927091700051X

Martín, B., Alonso, J. C., Martín, C. a., Palacín, C., Magaña, M., & Alonso, J. A. (2012). Influence of spatial heterogeneity and temporal variability in habitat selection: A case study on a great bustard metapopulation. *Ecological Modelling*, **228**, 39–48. doi:10.1016/j.ecolmodel.2011.12.024

Martín, C. A., Alonso, J. C., Alonso, J. A., Palacín, C., Magaña, M., & Martín, B. (2007). Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard *Otis tarda*. *Journal of Avian Biology*, **38**, 335–346. doi:10.1111/j.2007.0908-8857.03811.x

Martín, C. A., Alonso, J. C., Alonso, J. A., Palacín, C., Magaña, M., & Martín, B. (2008). Natal dispersal in great bustards: the effect of sex, local population size and spatial isolation. *Journal of Animal Ecology*, *77*(2), 326–334. doi:10.1111/j.1365-2656.2007.01349.x

Michael, P. E., Thomson, R., Barbraud, C., Delord, K., De Grissac, S., Hobday, A. J., … Wilcox, C. (2017). Illegal fishing bycatch overshadows climate as a driver of albatross population decline. *Marine Ecology Progress Series*, **579**, 185–199. doi:10.3354/meps12248

Morales, M. B., Alonso, J. C., Alonso, J. A., & Martín, E. (2000). Migration patterns in male great bustards (*Otis tarda*). *Auk*, **117**, 493–498.

Morales, M. B., Jiguet, F., & Arroyo, B. (2001). Exploded leks: What bustards can teach us. *Ardeola*, **48**, 85–98.

Moreira, F., Leitão, P. J., Morgado, R., Alcazar, R., Cardoso, A., Carrapato, C., … Osborne, P. E. (2007). Spatial distribution patterns, habitat correlates and population estimates of steppe birds in Castro Verde. *Airo*, **17**, 5–30.

Moreira, F., Leitão, P. J., Synes, N. W., Alcazar, R., Catry, I., Carrapato, C., … Osborne, P. E. (2012). Population trends in the steppe birds of Castro Verde in the period 2006-2011: Consequences of a drought evens and land use changes? *Airo*, **22**, 79–89.

Moreno, V., Morales, M. B., & Traba, J. (2010). Avoiding over-implementation of agri-environmental schemes for steppe bird conservation: a species-focused proposal based on expert criteria. *J Environ Manage*, **91**, 1802–1809. doi:10.1016/j.jenvman.2010.03.018

Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C., & Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, **19**, 478–486. doi:10.1111/ele.12584

Palacín, C., & Alonso, J. C. (2018). Failure of EU Biodiversity Strategy in Mediterranean farmland protected areas. *Journal for Nature Conservation*, **42**, 62–66. doi:10.1016/j.jnc.2018.02.008

Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (1999). Dispersal and spatial scale affect synchrony in spatial population dynamics. *Ecology Letters*, **2**, 114–120. doi:10.1046/j.1461-0248.1999.22060.x

Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (2000). Spatial synchrony in populations of birds: Effects of habitat , population trend, and spatial scale. *Ecology*, **81**, 2112–2125.

PCEBMS. (2016). European wild bird indicators, 2016 update. Retrieved March 20, 2018, from http://www.ebcc.info/index.php?ID=612/

Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., … Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, **344**, 1090–1092. doi:10.1126/science.1253425

Pinto, M., Rocha, P., & Moreira, F. (2005). Long-term trends in great bustard (*Otis tarda*) populations in Portugal suggest concentration in single high quality area. *Biological Conservation*, **124**, 415–423. doi:10.1016/j.biocon.2005.01.047

Reino, L., Porto, M., Morgado, R., Moreira, F., Fabião, A., Santana, J., … Beja, P. (2010). Effects of changed grazing regimes and habitat fragmentation on Mediterranean grassland birds. *Agriculture, Ecosystems and Environment*, **138**, 27–34. doi:10.1016/j.agee.2010.03.013

Ribeiro, P. F., Santos, J. L., Bugalho, M. N., Santana, J., Reino, L., Beja, P., & Moreira, F. (2014). Modelling farming system dynamics in High Nature Value Farmland under policy change. *Agriculture, Ecosystems and Environment*, **183**, 138–144. doi:10.1016/j.agee.2013.11.002

Rocha, P., Marques, A. T., & Moreira, F. (2005). Seasonal variation in Great Bustard *Otis tarda* diet in south Portugal with a focus on the animal component. *Ardeola*, **52**, 371–376.

Rocha, P., Morales, M. B., & Moreira, F. (2012). Nest site habitat selection and nesting performance of the great bustard *Otis tarda* in southern Portugal: Implications for conservation. *Bird Conservation International*, **23**, 323–336. doi:10.1017/s0959270912000202

Sæther, B.-E., & Bakke, O. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**, 642–653.

Santana, J., Reino, L., Stoate, C., Borralho, R., Carvalho, C. R., Schindler, S., … Beja, P. (2014). Mixed effects of long-term conservation investment in Natura 2000 farmland. *Conservation Letters*, **7**, 467–477. doi:10.1111/conl.12077

Santos, M., Bessa, R., Cabral, J. A., Pacheco, F. A. L., Leitão, D., Moreira, F., Pinto, M., Lecoq, M., & Silva, J. P. (2016). Impacts of land use and infrastructural changes on threatened Little Bustard *Tetrax tetrax* breeding populations: Quantitative assessments using a recently developed spatially explicit dynamic modelling framework. *Bird Conservation International*, **26**. doi:10.1017/S0959270915000258

Silva, J. P., Correia, R., Alonso, H., Martins, R. C., D'Amico, M., Delgado, A., … Moreira, F. (2018). EU protected area network did not prevent a country wide population decline in a threatened grassland bird. *PeerJ*, **6**, e4284. doi:10.7717/peerj.4284

Silva, J. P., Santos, M., Queirós, L., Leitão, D., Moreira, F., Pinto, M., … Cabral, J. A. (2010). Estimating the influence of overhead transmission power lines and landscape context on the density of little bustard *Tetrax tetrax* breeding populations. *Ecological Modelling*, **221**, 1954–1963. doi:10.1016/j.ecolmodel.2010.03.027

Stoate, C., Báldi, A., Beja, P., Boatman, N. D., Herzon, I., van Doorn, A., … Ramwell, C. (2009). Ecological impacts of early 21st century agricultural change in Europe - A review. *Journal of Environmental Management*, **91**, 22–46. doi:10.1016/j.jenvman.2009.07.005

Suárez, F., Naveso, M. A., & De Juana, E. (1997). Farming in the drylands of Spain: birds of the pseudosteppes. In D. J. Pain & M. W. Pienkowski (Eds.), *Farming and Birds in Europe. The Common Agricultural Policy and its Implications for Bird Conservation.* (pp. 297–330). San Diego: Academic Press.

Tarjuelo, R., Morales, M., Arroyo, B., Mañosa, S., Bota, G., Casas, F., & Traba, J. (2017). Intraspecific and interspecific competition induces dependent habitat niche shifts in an endangered steppe bird. *Ecology and Evolution*, **7**, 1–11. doi:10.1002/ece3.3444

Tarjuelo, R., Morales, M. B., Traba, J., & Delgado, M. P. (2014). Are species coexistence areas a good option for conservation management? Applications from fine scale modelling in two steppe birds. *Plos One*, **9**, 1–9. doi:10.1371/journal.pone.0087847.g001

Tarjuelo, R., Traba, J., Morales, M. B., & Morris, D. W. (2016). Isodars unveil asymmetric effects on habitat use caused by competition between two endangered species. *Oikos*, **126,** 73-81. doi:10.1111/oik.03366

Tuck, G. N., Polacheck, T., Croxall, J. P., & Weimerskirch, H. (2001). Modelling the impact of fishery bycatch on albatross populations: Model specification. *Journal of Applied Ecology*, **38**, 1182–1196.

Wade, A. S. I., Barov, B., Burfield, I. J., Gregory, R. D., Norris, K., Vorisek, P., … Butler, S. J. (2014). A niche-based framework to assess current monitoring of European forest birds and guide indicator species' selection. *PLoS ONE*, **9**, e97217. doi:10.1371/journal.pone.0097217